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Pucadelphys andinus (Marsupialia, Mammalia) from the early Paleocene of Bolivia

Larry G. MARSHALL, Christian de MUIZON & Denise SIGOGNEAU-RUSSELL

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MÉMOIRES DU MUSÉUM NATIONAL D'HISTOIRE NATURELLE

TOME 165
PALÉONTOLOGIE

Pucadelphys andinus *(Marsupialia, Mammalia) from the early Paleocene of Bolivia*

Larry G. MARSHALL*, Christian DE MUIZON**, Denise SIGOGNEAU-RUSSELL***

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Published November 27th 1995.

The specimens of *Pucadelphys andinus* studied in this volume were collected in the early Paleocene beds of the Santa Lucía Formation at Tiupampa (Bolivia). In this first part, a short presentation is given of the locality of Tiupampa, of the horizon from which the skeletons of *Pucadelphys andinus* were collected and of their age. We also provide an updated list of the mammalian fauna yielded by the site, and present comments on the taphonomy and paleoenvironment of the oldest known undoubted marsupial skeletons.

MARSHALL, L. G., MUIZON C. DE, 1995.— Part II: The skull *In*: C. DE MUIZON (ed.), *Pucadelphys andinus* (Marsupialia, Mammalia) from the early Paleocene of Bolivia. *Mém. Mus. natn. Hist. nat.*, **165** : 21-90. Paris ISBN : 2-85653-223-3.

Published November 27th 1995.

One of the earliest known complete dentitions and skulls of a metatherian mammal are represented by *Pucadelphys andinus* MARSHALL & MUIZON (1988) from the Early Paleocene age Santa Lucía Formation at Tiupampa (type locality of the Tiupampan Land Mammal Age) in southcentral Bolivia. A detailed analysis of the dentition, dentary and skull reveals that the vast majority of states in *Pucadelphys* can be regarded as mammalian and/or tribosphenid plesiomorphies, while metatherian synapomorphies include: cheek tooth formula of P3/3 +M4/4; prootic canal reduced in length and width, and does not open endocranially; prootic sinus continues onto squamosal side of petromastoid within a deep sulcus; presence of sphenoparietal emissary vein which occupies deep sulcus on squamosal side of petromastoid, is continuous with sulcus for prootic sinus, and exits skull through postglenoid foramen; length/width ratio of fenestra vestibuli 1.4; and absence of stapedial artery. *Pucadelphys* lacks an ossified alisphenoid bulla, but has what is interpreted to be a small anterior lamina of the petromastoid and a large foramen ovale (exit of V3) which opens between the anterior lamina and alisphenoid. The presence of an anterior lamina of the petromastoid fused to the pars petrosa associated to the presence of an anteroposteriorly expanded alisphenoid in *Pucadelphys* seems to contradict the hypothesis of PRESLEY & STEEL (1976) and PRESLEY (1981) on the evolution of the tribosphenid middle ear and lateral wall of the skull based on ontogenetic studies. This is the first record of an anterior lamina in a tribosphenid fossil mammal. The molar structure of *Pucadelphys* is indistinguishable from members of the family Didelphidae, and it is placed in this family, within the Order Didelphimorphia. *Pucadelphys* represents an intriguing example of mosaic evolution and illustrates that we have much to learn about early metatherian and tribosphenid evolution.

MARSHALL, L. G. & SIGOGNEAU-RUSSELL, D., 1995.— Part III: Postcranial skeleton. *In:* C. DE MUIZON (ed.), *Pucadelphys andinus* (Marsupialia, Mammalia) from the early Paleocene of Bolivia. *Mém. Mus. natn. Hist. nat.*, **165** : 91-164. Paris ISBN : 2-85653-223-3.

Published November 27th 1995.

The earliest and most complete articulated skeletons of fossil metatherians yet known are represented by four specimens of *Pucadelphys andinus* from the Santa Lucía Formation (early Paleocene) at Tiupampa in southcentral Bolivia. Two sets of what are interpreted to be male-female pairs were found in a three dimensional, life-like, snout-rump position in burrow-nests that were apparently dug in a bank along a meandering river. The animals apparently died as the result of a flood which entrapped them in their burrows and filled the latter with water and sediment. A detailed comparative study of the postcranial bones reveals that the vast majority of character states in *Pucadelphys* are regarded as mammalian, tribosphenic or metatherian plesiomorphies (e.g. atlas not perforated by transverse canal and with a persisting suture between ossified intercentrum and atlantal arch; absence of transverse canal on axis, with possible unfused rib; absence of enclosed transverse canal on CV7; robust fibula; presence of ossified os marsupium; etc.). Character states of uncertain polarity include the presence of only one vertebra articulating with the ilium (fulcral vertebra), and a long non-prehensile tail. The tarsus has a bicontact upper ankle joint (UAJ) as in living Didelphidae; moreover the calcaneum shows a partially plantar orientation of the cuboid facet which can be interpreted as foreshadowing the specialisation of later Didelphidae; the situation then is more advanced than in the "plesiomorphic metatherian morphotype" of SZALAY (1982 a, b; 1984); the only characters of the latter persisting in *Pucadelphys* are the large peroneal process and the "remarkably broad transverse dimensions from peroneal process to the medial margin of the sustentaculum". Collectively these characters support the view, based on the study of the skull and dentition (MARSHALL & MUIZON, this volume), that *Pucadelphys* represents the plesiomorphic taxon within the family Didelphidae. Functional considerations of the skeletons suggest that *Pucadelphys* was essentially terrestrial, quite agile, and possessed limited bounding and digging capabilities.

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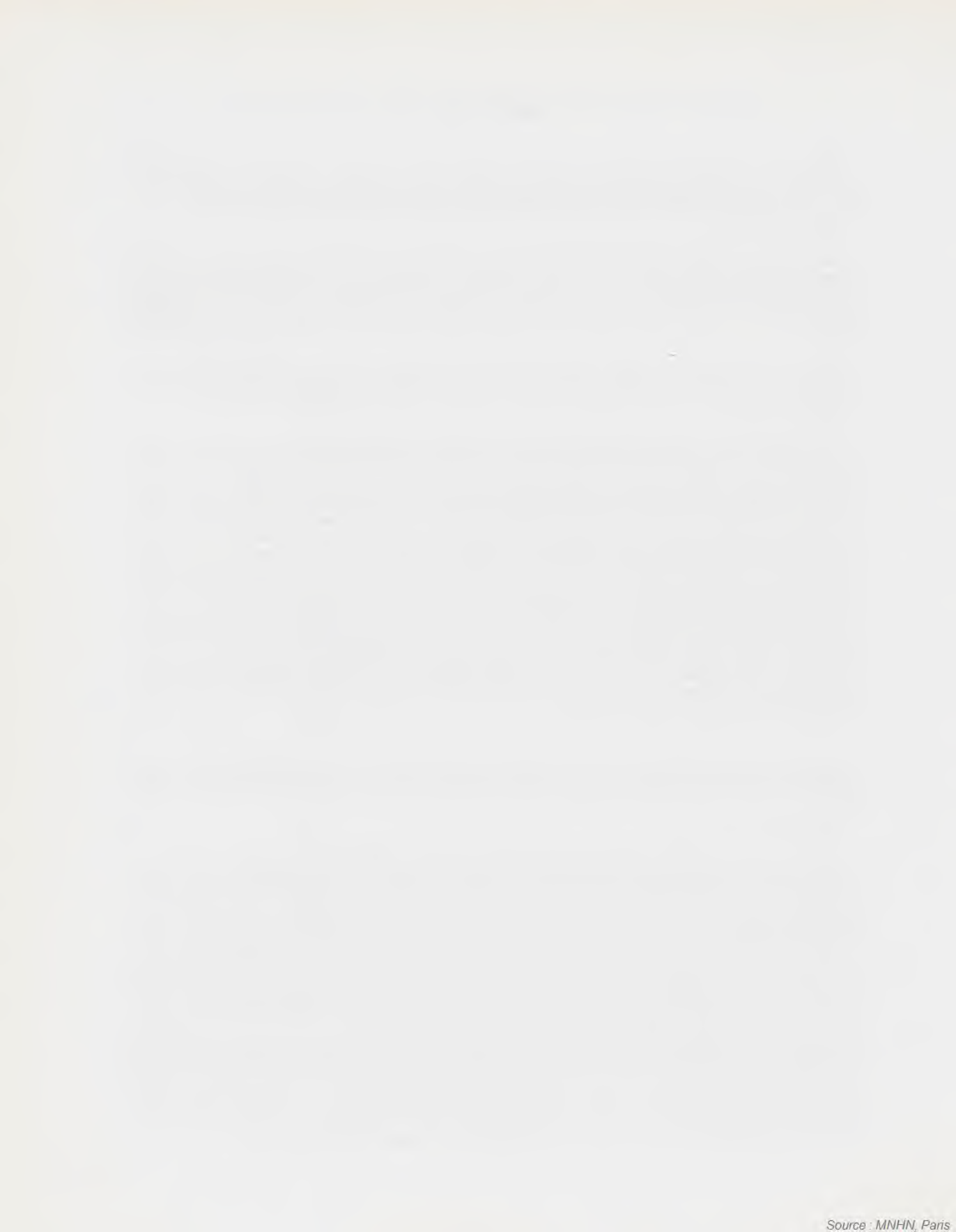

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Part I: The locality of Tiupampa: age, taphonomy and mammalian fauna

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ABSTRACT

The specimens of *Pucadelphys andinus* studied in this volume were collected in the early Paleocene beds of the Santa Lucía Formation at Tiupampa (Bolivia). In this first part, a short presentation is given of the locality of Tiupampa, of the horizon from which the skeletons of *Pucadelphys andinus* were collected and of their age. We also provide an updated list of the mammalian fauna yielded by the site, and present comments on the taphonomy and paleoenvironment of the oldest known undoubted marsupial skeletons.

RÉSUMÉ

Première partie : le gisement de Tiupampa : âge, taphonomie et faune de mammifères

Les spécimens de *Pucadelphys andinus* qui font l'objet de ce mémoire ont été récoltés dans des niveaux du Paléocène ancien de la Formation Santa Lucía à Tiupampa (Bolivie). Cette première partie offre une brève présentation de la localité de Tiupampa, de l'horizon d'où proviennent les squelettes et de leur âge. Elle contient aussi une liste mise à jour de la faune mammalienne d'accompagnement, ainsi que des informations sur la taphonomie et le paléoenvironnement de ces squelettes de marsupiaux, qui sont les plus anciens actuellement connus.

MARSHALL, L. G., MUIZON, C. DE & SIGOGNEAU-RUSSELL, D., 1995.— Part I: The locality of Tiupampa: age, taphonomy and mammalian fauna. *In*: MUIZON, C. DE (ed.), *Pucadelphys andinus* (Marsupialia, Mammalia) from the early Paleocene of Bolivia. *Mém. Mus. natn. Hist. nat.*, **165** : 11-20. Paris ISBN : 2-85653-223-3.

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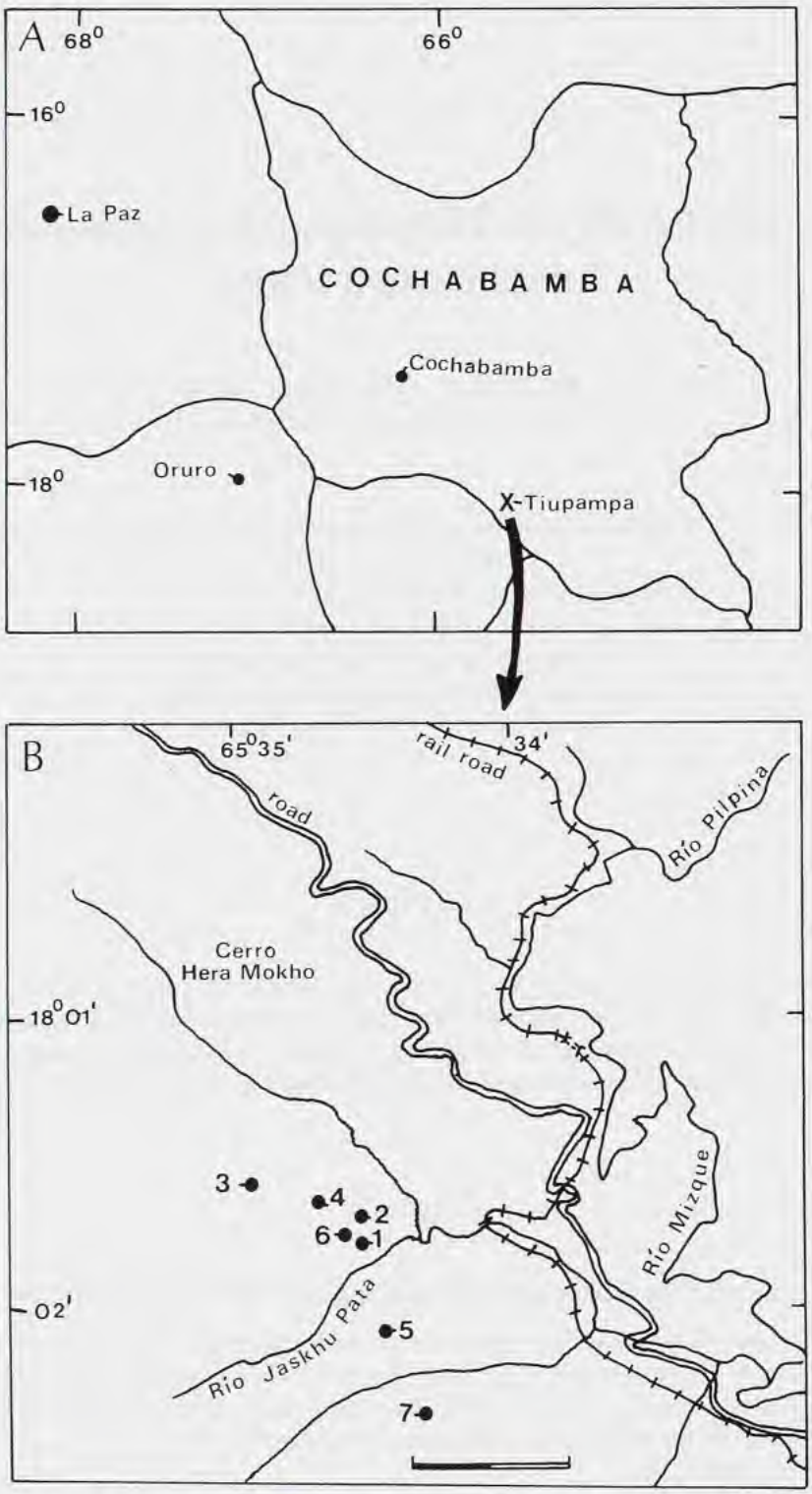

FIG. 1. — Map of southcentral Bolivia showing location of Tiupampa (top) and detail map of Tiupampa area showing fossil vertebrate sites (bottom). The skeletons of *Pucadelphys andinus* are from site 1 ("the quarry").

FIG. 1. — Carte de la partie sud du centre de la Bolivie montrant la situation de Tiupampa (en haut), et carte détaillée de la région de Tiupampa montrant les localités à vertébrés fossiles (en bas). Les squelettes de Pucadelphys andinus *proviennent de la localité 1 ("the quarry").*

Source : MNHN, Paris

The locality of Tiupampa, recognized as a promising site as early as 1980 by R. HOFFSTTETER, C. DE MUIZON and P. TAQUET, yielded its first mammalian remains (a marsupial) during a second campaign (1982) organized in particular by L. G. MARSHALL and Ch. DE MUIZON. It was in the course of a 4th campaign (1985) that the skeletons of *Pucadelphys andinus* presented here were found.

LOCALITY, HORIZON, AND AGE

These specimens were recovered from the Santa Lucía Formation (*sensu* GAYET *et al.*, 1992; MUIZON, 1992; MUIZON & BRITO, 1993) at Tiupampa, located about 95km southeast of Cochabamba (65°35'W, 18°02'S), Mizque Province, Department of Cochabamba, southcentral Bolivia (Fig. 1, top). Details of the topography are shown on Carta Nacional Boliviana San Vicente Quadrangle, Hoja 6439 1, serie H731, 1/50,000, 1968. All specimens are from site 1 ("the quarry") (Fig. 1, bottom).

The rich and taxonomically diverse vertebrate fauna discovered at Tiupampa in 1982 was initially believed to be from the "Late Cretaceous" age El Molino Formation (MARSHALL *et al.*, 1983; 1985; MUIZON *et al.*, 1983, 1984; MARSHALL & MUIZON, 1988). However, recent detailed studies of the biostratigraphy (GAYET *et al.*, 1992) and stratigraphy (SEMPERE, 1994) of the El Molino and overlying Santa Lucía Formations reveal the following: 1) uncontested Late Cretaceous age "guide" fossils (i.e. dinosaurs, some selachians and fish) occur only in the lower and basal middle members of the El Molino Formation, which collectively span early and late Maastrichtian times; 2) the upper member of the El Molino Formation is Early Paleocene (Danian); 3) the K/T boundary lies in the upper part of the middle member of the El Molino Formation; but, another interpretation is given by JAILLARD *et al.* (1993: 650) who definitely consider the El Molino Formation as a lateral equivalent of the Upper Vilquechico Formation from Peru, which they ascribed to a latest Campanian-late Maastrichtian interval (JAILLARD *et al.*, 1993: 655). The mammal-bearing level at Tiupampa, which has yielded the type fauna of the Tiupampian Land Mammal age, has been assigned to the Santa Lucía Formation (GAYET *et al.*, 1992; MUIZON, 1992; and MUIZON & BRITO, 1993) and has been given an early Paleocene age (ORTIZ JAUREGUIZAR & PASCUAL, 1989; MARSHALL, 1989; BONAPARTE *et al.*, 1993; MUIZON & BRITO, 1993). Finally, studies in progress on the geochronology of the El Molino and Santa Lucía Formations (SEMPÉRÉ & MARSHALL, in prep.; SEMPERE *et al.*, in prep.) would suggest an age slightly younger in the Paleocene than stated before. Pending formal publication of these results, the Tiupampa land mammal fauna and the Tiupampian land-Mammal age will be referred here to the early Paleocene following VAN VALEN (1988), MUIZON (1992), BONAPARTE *et al.* (1993), and MUIZON & BRITO (1993).

Stratigraphic sections showing the location of the fossil level in the Tiupampa section are provided by MUIZON *et al.* (1983, fig. 1) and MARSHALL *et al.* (1985, fig. 4, right).

TAPHONOMY

The Santa Lucía Formation at Tiupampa was deposited in channels of meandering rivers on a flat alluvial plain. The water-lain sediments surrounding the skeletons are a well-sorted, weakly

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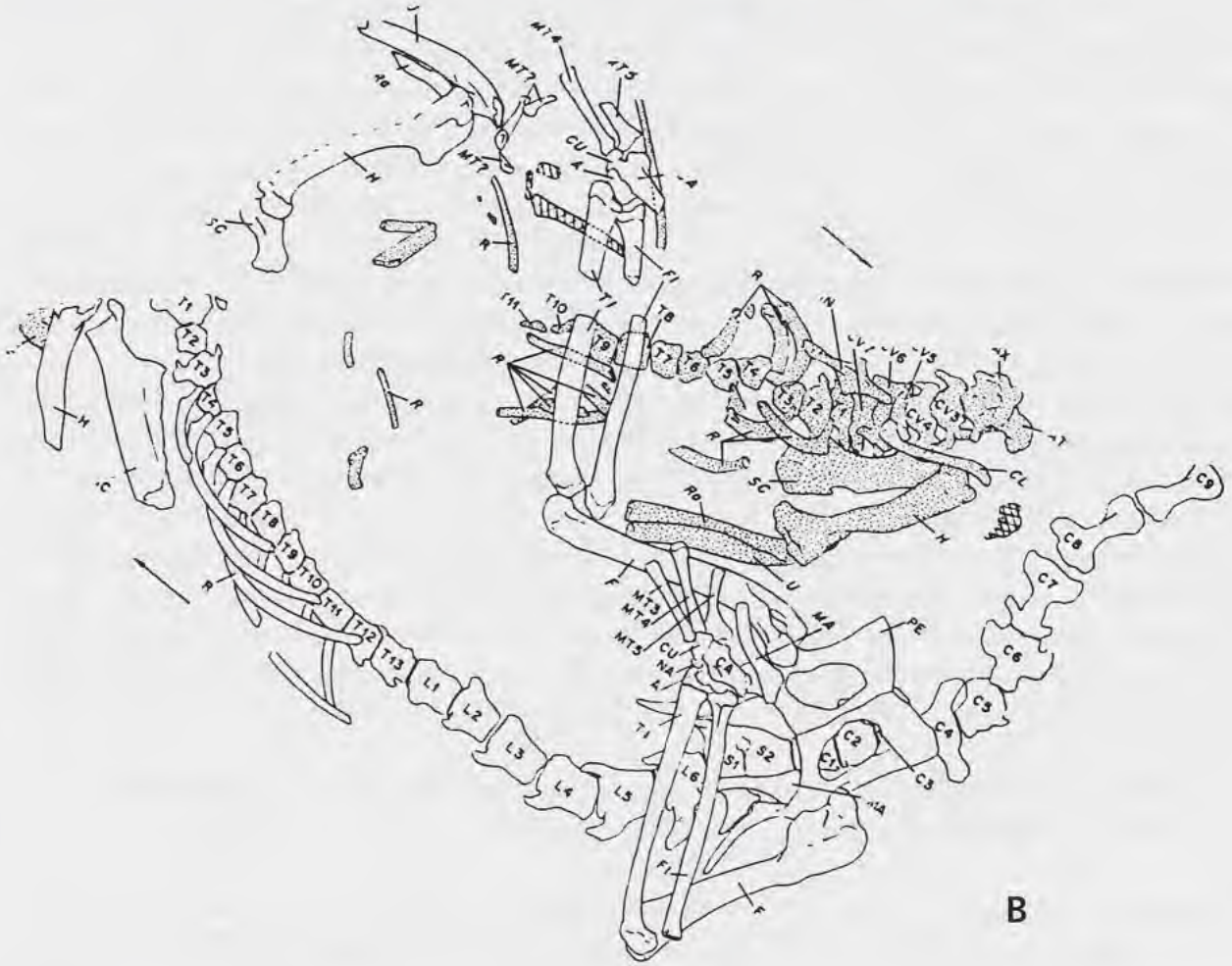
A



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consolidated, fine-grained quartzose-sandstone with sparse feldspar grains, some hematite and traces of red clay between the predominantly quartz grains. The red color comes from the iron dioxide. The presence of several taxa of crocodiles attests to a warm, probably subtropical, climate.

The specimens were collected from sediment blocks that had been transported about 2km from site 1 (Fig. 1, bottom) to a screen-washing location; they were first observed by P.-Y. GAGNIER. The blocks containing the skeletal remains were prepared at the MNHN by C. DE MUIZON and L. G. MARSHALL. This revealed that four partial skeletons were represented and that these occurred in pairs (6105 and 6106, 6110 and 6111, respectively; see below).

The individuals of each pair were apparently in a "snuggle" position and facing in opposite directions (Figs 3 and 4). We interpret this relationship to indicate that these animal-pairs (probably male and female, see below) were in burrow-nests and sleeping (or resting) in a snout-rump position typical of many living didelphids (see below). We further believe that these animals probably died as the result of a flood that entrapped them in their burrows and filled the latter with water and sediment. The "died-in-a-burrow" hypothesis is supported by the fact that frogs (some represented by complete skeletons, BAEZ, 1992) are abundant throughout "the quarry" fossil level, and that these apparently lived in a pond or oxbow adjacent to a bank that was used as a burrow-nest site; this interpretation would also explain the exceptionnally high number of fossils in this level, which may have died as a result of a single carastrophic flood (SEMPERE & MARSHALL, in prep.).

There was apparently little time lapse between death and the onset of fossilization (*i.e.* permanent entombment in the sediment). This is evidenced by the fact that the majority of bones are articulated, suggesting little or no postmortem dismemberment. Nevertheless, some rib fragments in both specimen-pairs are situated "out-of-context" of the main skeletons, no distal phalanges or claws are articulated with the four partial pes and only five caudal vertebrae posterior to C9 are preserved. These features are interpreted to indicate that some movement of sediment

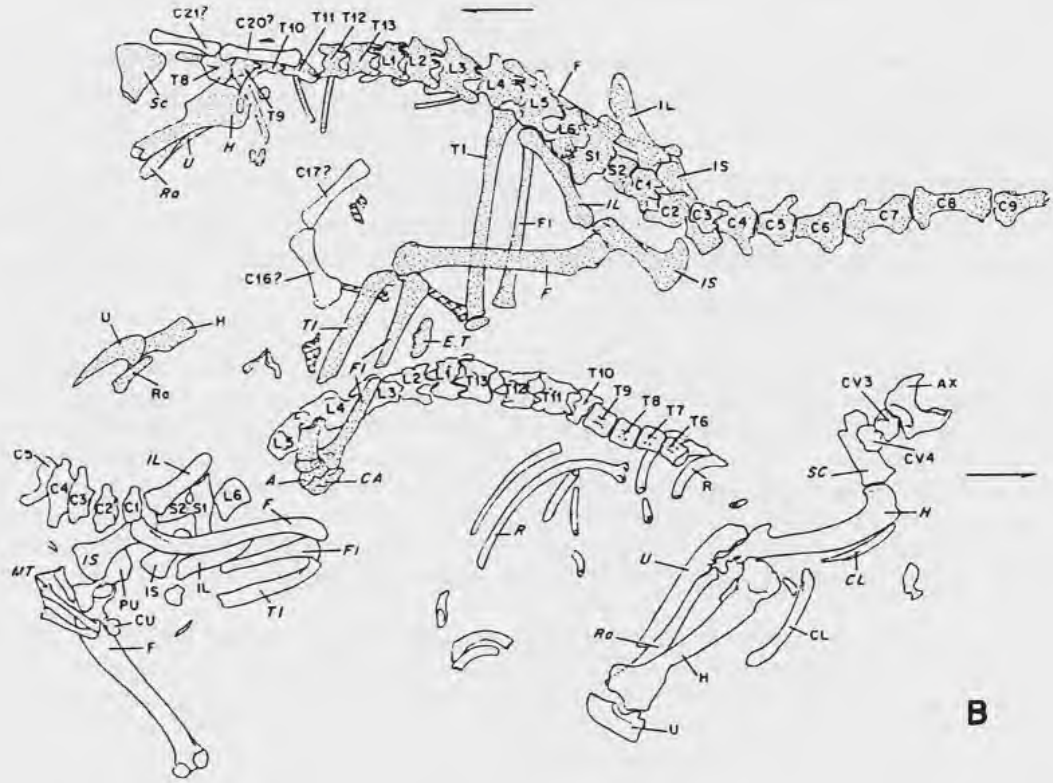
---

FIG. 2. — *Pucadelphys andinus*. A, specimen-pair YPFB Pal 6105, holotype, (top) and YPFB Pal 6106 (bottom) photographed at initial stage of preparation; 6105 faces right; 6106 faces left. X3/4. B, line-drawing of same specimen-pair after preparation (skull of YPFB Pal 6105 detached). Bones of YPFB Pal 6105 are stippled and bones of YPFB Pal 6106 are left white to facilitate identification and association. X 1,5. In Roman letters, unpaired bones and paired bones of the right side; in italics, paired bones of the left side; cross-hatched, unattributed bones. Abbreviations: **A**, astragalus; **AT**, atlas; **AX**, axis; **C**, caudal vertebra; **CA**, calcaneum; **CL**, clavicle; **CU**, cuboid; **CV**, cervical vertebra; **F**, femur; **FI**, fibula; **H**, humerus; **IL**, ilium; **IN**, interclavicle; **IS**, ischium; **L**, lumbar vertebra; **MA**, os marsupium; **MT**, metatarsal; **NA**, navicular; **PU**, pubis; **R**, rib; **RA**, radius; **S**, sacral vertebra; **SC**, scapula; **T**, thoracic vertebra; **TI**, tibia; **U**, ulna.

FIG. 2. — Pucadelphys andinus. *A, couple de spécimens (YPFB Pal 6105, holotype, en haut) et YPFB Pal 6106 (en bas) photographiés au début de la préparation: YPFB Pal 6105 est sur le côté droit, 6106 sur le côté gauche. X 3/4. B, dessin au trait des mêmes spécimens après préparation (le crâne de YPFB Pal 6105 a été retiré). X 1,5. Les os de YPFB Pal 6105 sont pointillés et ceux de YPFB Pal 6106 ont été laissés en blanc pour faciliter l'identification et les associations. En lettres romaines, os impairs et os pairs du côté droit; en italiques, os pairs du côté gauche; en hachures, os non attribués. Abréviations: **A**, astragale; **AT**, atlas; **AX**, axis, **C**, vertèbre caudale; **CA**, calcanéum; **CL**, clavicule; **CU**, cuboïde; **CV**, vertèbre cervicale; **F**, fémur; **FI**, fibula; **H**, humérus; **IL**, ilion; **IN**, interclavicule; **IS**, ischium; **L**, vertèbre lombaire; **MA**, os marsupial; **MT**, métatarsien; **NA**, naviculaire; **PU**, pubis; **R**, côte; **RA**, radius; **S**, vertèbre sacrée; **SC**, scapula; **T**, vertèbre thoracique; **TI**, tibia; **U**, cubitus.*

Source : MNHN, Paris

A



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around the corpses occurred, causing minor displacement and/or loss of some fragile extremity bone elements. Diagenetic processes were, however, exceedingly weak as evidenced by the facts that the sediments are poorly consolidated, the bones show no or only minor evidence of deformation, and the skulls and skeletons are preserved in a three dimensional, "life-like" state.

MAMMALIAN FAUNAL LIST

The Locality of Tiupampa has yielded an abundant mammalian fauna. An updated list (modified from MUIZON, 1992 and MUIZON & BRITO, 1993) is given below:

Class Mammalia
- Infra-class Metatheria
  - Order Sparassodonta
    - Family Hathliacynidae
      - *Allqokirus australis* Marshall & Muizon, 1988
    - Family Mayulestidae
      - *Mayulestes ferox* Muizon, 1994
  - Order Peradectia
    - Family Peradectidae
      - *Peradectes cf. austrinum*
      - *Roberthoffstetteria nationalgeographica* Marshall, Muizon & Sigé, 1983
  - Order Microbiotheria
    - Family Microbiotheriidae
      - *Khasia cordillerensis* Marshall & Muizon, 1988

FIG. 3. — *Pucadelphys andinus*. A, specimen-pair YPFB Pal 6110 (bottom) and YFPB Pal 6111 (top) photographed at initial stage of preparation. YPFB Pal 6110 faces right; YPFB Pal 6111 faces left. X 3/4. B, line drawing of same specimen-pair after preparation (skull of YPFB Pal 6110 detached). X 1,5. Bones of YPFB Pal 6111 are stippled and bones of YPFB Pal 6110 are left white to facilitate identification and association. In Roman letters, unpaired and paired bones of the right side; in italics, paired bones of the left side; cross-hatched, unattributed bones. In the part of YPFB Pal 6110 corresponding to Fig. 4, bones are drawn reversed. For abbreviations, see caption to Fig. 2.

FIG. 3. — Pucadelphys andinus. *A, couple de spécimens YPFB Pal 6110 (en bas) et YPFB Pal 6111 (en haut) photographiés au début de la préparation. YPFB Pal 6110 est sur le côté droit; YPFB Pal 6111 sur le côté gauche. X 3/4; B, dessin au trait des mêmes spécimens après préparation (le crâne de YPFB Pal 6110 a été retiré). X 1,5. Les os de YPFB Pal 6111 sont pointillés et ceux de YPFB Pal 6110 ont été laissés en blanc pour faciliter l'identification et les associations. En lettres romaines, os impairs et os pairs du côté droit; en italiques, os pairs du coté gauche; en hachures, os non attribués. Sur la partie de YPFB Pal 6110 correspondant à la Fig. 4, le dessin a été renversé. Pour les abréviations, voir légende Fig. 2.*

Source : MNHN, Paris

Order Didelphimorphia
Family Didelphidae
Pucadelphys andinus Marshall & Muizon, 1988
Incadelphys antiquus Marshall & Muizon, 1988
Mizquedelphys pilpinensis Marshall & Muizon, 1988
Andinodelphys cochabambensis Marshall & Muizon, 1988
Tiulordia floresi Marshall & Muizon, 1988
Family Jaskhadelphydae
Jaskhadelphys minutus Marshall & Muizon, 1988
Infra-class Eutheria
Order Leptictida
Family Palaeoryctidae?
cf. *Cimolestes* sp.
Family indet.
Gen. and sp. indet.
Order Pantodonta
Family Alcidedorbignyidae
Alcidedorbignya inopinata MUIZON & Marshall, 1987
Order Condylarthra
Family Mioclaenidae
Molinodus suarezi Muizon & Marshall, 1987
Tiuclaenus minutus Muizon & Marshall,1987
Tiuclaenus sp. nov. 1
Tiuclaenus sp. nov.2
Pucanodus gagnieri Muizon & Marshall, 1991
Mioclaenidae nov. gen., nov. sp.
Family Mioclaenidae or Didolodontidae
Andinodus boliviensis Muizon & Marshall, 1987
Family ?Periptychidae
aff. ?*Mimatuta*
Order Condylarthra *incertae sedis*
Family Kollpaniidae
Kollpania tiupampina Marshall & Muizon, 1988
Order Notoungulata
Family Henricosborniidae or Oldfiedthomasiidae

ABBREVIATIONS OF INSTITUTIONS

MNHN, Laboratoire de Paléontologie, Muséum national d'Histoire naturelle, Paris, France. YPFB Pal, Paleontology collection of Yacimientos Petrolíferos Fiscales de Bolivia in the Centro de Tecnología Petrolera, Santa Cruz, Bolivia.

Source : MNHN, Paris

FIG. 4. — *Pucadelphys andinus*. YPFB Pal 6110, reversed photo (X 3) of accessory block, to show its continuity with main block in Fig. 3 (see explanation Fig. 26).

FIG. 4. — Pucadelphys andinus. *YPFB Pal 6110, photo renversée (X 3) du bloc accessoire, pour montrer la continuité avec le bloc principal de la Fig. 3 (voir explication Fig. 26).*

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Source : MNHN, Paris

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Source : MNHN, Paris

Part II: The skull

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ABSTRACT

One of the earliest known complete dentitions and skulls of a metatherian mammal are represented by *Pucadelphys andinus* Marshall & Muizon, (1988) from the early Paleocene age Santa Lucía Formation at Tiupampa (type locality of the Tiupampan Land Mammal Age) in southcentral Bolivia. A detailed analysis of the dentition, dentary and skull reveals that the vast majority of states in *Pucadelphys* can be regarded as mammalian and/or tribosphenid plesiomorphies, while metatherian synapomorphies include: cheek tooth formula of P3/3+ M4/4; prootic canal reduced in length and width, and does not open endocranially; prootic sinus continues onto squamosal side of petromastoid within a deep sulcus; presence of sphenoparietal emissary vein which occupies deep sulcus on squamosal side of petromastoid, is continuous with sulcus for prootic sinus, and exits skull through postglenoid foramen; length/width ratio of fenestra vestibuli 1.4; and absence of stapedial artery. *Pucadelphys* lacks an ossified alisphenoid bulla, but has what is interpreted to be a small anterior lamina of the petromastoid and a large foramen ovale (exit of V3) which opens between the anterior lamina and alisphenoid. The presence of an anterior lamina of the petromastoid fused to the pars petrosa associated to the presence of an anteroposteriorly expanded alisphenoid in *Pucadelphys* seems to contradict the hypothesis of Presley & Steel (1976) and Presley (1981) on the evolution of the tribosphenid middle ear and lateral wall of the skull based on ontogenetic studies. This is the first record of an anterior lamina in a tribosphenid fossil mammal. The molar structure of *Pucadelphys* is indistinguishable from members of the family Didelphidae, and it is placed in this family, within the Order Didelphimorphia. *Pucadelphys* represents a classic example of mosaic evolution and illustrates that we have much to learn about early metatherian and tribosphenid evolution.

Marshall, L. G., Muizon C. de, 1995.— Part II: The skull. *In*: Muizon, C. de (ed.), *Pucadelphys andinus* (Marsupialia, Mammalia) from the early Paleocene of Bolivia. *Mém. Mus. natn. Hist. nat.*, **165** : 21-90. Paris ISBN : 2-85653-223-3.

Source : MNHN, Paris

RÉSUMÉ

Deuxième partie : le crâne

Les crânes et dentitions de *Pucadelphys andinus* MARSHALL & MUIZON, (1988) décrits dans ce travail sont parmi les plus anciens connus chez les métathériens. Ils proviennent du Paléocène inférieur de la Formation Santa Lucía à Tiupampa (localité-type de l'âge de mammifères continentaux, Tiupampien) en Bolivie centrale. Une analyse détaillée de la dentition, du dentaire et du crâne révèle que la grande majorité des états de *Pucadelphys* peuvent être considérés comme des plésiomorphies au sein de mammifères et/ou des tribosphénides. Les synapomorphies de métathérien sont : dents jugales au nombre de P 3/3 et M 4/4; canal prootique réduit en longueur et en largeur, ne s'ouvrant pas à l'intérieur du crâne; sinus prootique se prolongeant sur la face squamosale du pétromastoïde dans un profond sillon; présence d'une veine émissaire sphénopariétale occupant un profond sillon sur la face squamosale du pétromastoïde, en continuité avec le sillon pour le sinus prootique et sortant du crâne à travers le foramen postglénoïde; rapport longueur/largeur de la fenêtre vestibulaire de 1,4; absence d'artère stapédiale. *Pucadelphys* ne possède pas de processus tympanique de l'alisphénoïde mais possède une petite lame antérieure du pétromastoïde et un grand foramen ovale (sortie du V3) qui s'ouvre entre la lame antérieure et l'alisphénoïde. La présence, chez *Pucadelphys*, d'une lame antérieure du pétromastoïde fusionnée à la pars petrosa et associée à la présence d'un alisphénoïde dilaté antéro-postérieurement, semble contredire l'hypothèse de PRESLEY & STEEL (1981) et PRESLEY (1981) sur l'évolution de l'oreille moyenne et de la paroi crânienne des tribosphénides, fondée sur des études ontogénétiques. Il s'agit du premier signalement d'une lame antérieure du pétromastoïde chez un mammifère tribosphénide fossile. La structure des molaires de *Pucadelphys* est indifférenciable de celle des membres de la famille des Didelphidae et ce genre est rangé dans cette famille au sein de l'ordre des Didelphimorphia. *Pucadelphys* représente un exemple classique d'évolution en mosaïque et illustre bien que nous avons encore beaucoup à apprendre sur les débuts de l'évolution des métathériens et des tribosphénides.

RÉSUMÉ DÉVELOPPÉ

Les os crâniens et basicrâniens de mammifères sont des éléments très importants dans les reconstructions phylogénétiques. Toutefois, très peu de crânes de mammifères tribosphénides sont connus pour le mésozoïque et le Paléocène inférieur et aucun crâne de métathérien incontesté n'est connu au mésozoïque. Plusieurs squelettes et crânes d'un marsupial Didelphidae (*Pucadelphys andinus*) ont été découverts dans le Paléocène inférieur de la Formation Santa Lucía (Bolivie) et constituent, avec celui de *Mayulestes ferox* (un borhyaenoïde provenant du même gisement), les plus anciens crânes complets connus rattachés avec sécurité à ce groupe de mammifères.

Dans ce travail nous présentons une description détaillée des crânes de *Pucadelphys andinus* MARSHALL & MUIZON (1988), nous discutons ses principaux caractères crâniens et les analysons dans une optique orientée vers la compréhension de la phylogénie des tribosphénides (Marsupiaux et Placentaires). Sont décrits successivement les dents supérieures, les dents inférieures, le dentaire et le crâne.

Famille Didelphidae
Pucadelphys andinus MARSHALL & MUIZON, 1988

DESCRIPTION

La formule dentaire de *Pucadelphys andinus* est I 5/4, C1/1, P 3/3, M4/4. Les incisives supérieures sont disposées en série continue et sont jointives. Elles sont croissantes de I1 à I4 et I5 est réduite. Les prémolaires sont biradiculées et présentent une forte augmentation de taille de P1 à P3. Elles ont une couronne simple constituée d'une grande cuspide triangulaire et d'un minuscule talon postérieur. La P3 est haute et sa couronne descend nettement plus bas que le plan occlusal des molaires. Les molaires supérieures sont triangulaires et présentent un paracône plus petit que le métacône (pour M1-M3), une centrocrista en V et un protocône relativement gros avec un bord postérieur renflé. La métacrista est petite mais légèrement plus grande que la paracrista. La plateforme stylaire est développée et possède des styles bien marqués. Les incisives inférieures sont de taille croissante de i1 à i4 et sont jointives. Les prémolaires inférieures sont semblables aux supérieures. Les molaires inférieures possèdent un trigonide élevé plus large que long. Le protoconide est légèrement plus grand que le métaconide, lequel est nettement plus développé que

Source : MNHN, Paris

le paraconide. La protocristide, droite et tranchante, est orientée transversalement. Le talonide possède un bassin profond et des cuspides bien marquées, entoconide et hypoconulide étant distinctement accolés. Le dentaire présente une branche horizontale longue et gracile, une fosse massétérine peu profonde, un vaste processus coronoïde et un condyle situé au-dessus du plan occlusal. Le crâne possède un museau court et obtus. Les arcades zygomatiques sont grandes et montrent une orbite en communication avec la fosse temporale. Il possède une légère crête sagittale pariétale et une crête lambdoïde marquée. Les nasaux sont allongés et présentent un forte dilatation de leur extrémité postérieure. Les prémaxillaires sont graciles et sont perforés ventralement par des foramens incisifs allongés, lesquels affectent également les maxillaires. L'arc dentaire est presque semi-circulaire. Les maxillaires possèdent une ouverture du canal infraorbitaire située au-dessus de P3. Le palatin possède un fort torus postpalatin situé en arrière de M5. En vue ventrale, maxillaires et palatins ne présentent pas de foramens palatins. Le lacrimal forme le bord antérieur de l'orbite; il est grand et s'étend largement sur la face dorsale du rostre. Le jugal est un os gracile, sigmoïde qui participe à l'élaboration de la cavité glénoïde. Le frontal occupe environ le tiers du crâne en vue dorsale et latérale. Il porte parfois un petit processus supraorbitaire et participe à la formation du foramen ethmoïdien. Le pariétal est une vaste plaque osseuse qui constitue la majeure partie du toit et des parois de la cavité crânienne. L'orbitosphénoïde est un os petit qui possède un grand foramen sphénorbitaire situé à sa jonction avec le frontal et le palatin. L'alisphénoïde forme la région antérieure et latérale de la boîte crânienne. Cet os participe à la formation de trois foramens. Le foramen ovale est énorme et se situe entre le bord postérieur de l'alisphénoïde et le bord antérieur du pétromastoïde, médialement à la cavité glénoïde. Antéro-médialement, le foramen entocarotidien est bordé latéralement par l'alisphénoïde et médialement par le basisphénoïde. Un foramen rotundum bien marqué s'observe antérieurement. Il n'existe pas de processus tympanique de l'alisphénoïde. Le squamosal présente une cavité glénoïde profonde et allongée transversalement, munie d'un grand processus postglénoïde et d'un petit processus préglénoïde. Le squamosal possède quatre foramens sur sa face externe : 1) le foramen postzygomatique, sur le bord postérieur de la racine postérieure de l'arcade zygomatique, dorsalement à l'apex du processus postglénoïde, 2) le foramen subsquamosal qui s'ouvre dorsalement au méat auditif externe, 3) le foramen postglénoïde, le plus grand, dont l'ouverture est située sur le flanc postérieur de la racine postérieure de l'arcade zygomatique, 4) le foramen posttemporal qui s'ouvre entre le squamosal et la pars mastoïdea du pétromastoïde. Ventralement, le squamosal participe à la formation du bord latéral du foramen ovale. Le pétromastoïde est un os complexe formé de la pars petrosa et la pars mastoidea. Cette dernière affleure largement sur la face postérieure du crâne entre l'exoccipital, le squamosal et le supraoccipital. Ventralement, la pars mastoidea participe à la formation de la moitié latérale du petit processus exoccipital et, latéralement, forme un processus mastoïde relativement grand. Le bord ventral de la pars mastoidea forme une lèvre dirigée antéro-ventralement qui constitue le processus tympanique caudal (*sensu* Wible, 1990). Il forme une partie du plancher du sinus mastoïde épitympanique. Une échancrure stylomastoïdienne bien marquée s'observe latéralement au processus mastoïde; elle donne passage au nerf facial et à la veine latérale de la tête. Le bord latéral du processus mastoïde s'étend antéro-dorsalement, séparant le bord latéral du sinus mastoïde épitympanique de la fossa incudis, située dans la région postérieure du récessus épitympanique. La pars petrosa présente un grand promontoire lisse et piriforme dont l'apex est dirigé antéro-médialement. Il est bordé antéro-médialement par un sinus marqué correspondant au passage de la carotide interne se dirigeant vers le foramen carotidien; latéralement au sinus carotidien se trouve la fosse du muscle tensor tympani. Le bord médial du promontoire présente un sillon interne marqué pour le passage du sinus pétreux inférieur. Sur la face latérale du promontoire, la fenêtre ovale se situe à la hauteur du bord postéro-dorsal du méat auditif externe; son rapport longueur/largeur est de 1,4. Antéro-latéralement à la fenêtre ovale, dans le sillon qui borde latéralement le promontoire, se trouve l'ouverture postérieure du canal facial secondaire. Latéralement à cette ouverture, se trouve un petit foramen, l'ouverture médiale du canal prootique. Le récessus épitympanique est une petite dépression allongée située latéralement au canal facial; son extrémité postérieure est la fossa incudis. Sur la face dorsale ou cérébelleuse du pétromastoïde s'observe une grande fossa subarcuata et le méat auditif interne. Quatre sillons entourent le corps du pétromastoïde sur sa face cérébellaire : 1) ventro-médialement, le sillon pour le sinus pétreux inférieur, 2) postéro-ventralement, un sillon vertical pour le sinus jugulaire, 3) postéro-dorsalement une petite poche représente le sillon pour le sinus sigmoïde, 4) le long du bord dorso-latéral se trouve un sillon allongé pour le sinus prootique. Antéro-latéralement à la crista petrosa, dans une aile osseuse se projetant antéro-dorsalement, se trouve une dépression pour le lobe temporal du cerveau et le ganglion trigéminé. Chez les autres Didelphidae le ganglion repose sur l'alisphénoïde et il n'existe pas de projection osseuse. Cette aile antéro-latérale du pétromastoïde contribue au plancher et au bord interne de la paroi crânienne. Elle représente apparemment une relique de la lame antérieure du pétreux (*sensu* Crompton & Jenkins, 1979). Sur la face ventrale du pétromastoïde, un contact irrégulier s'observe entre le bord antéro-latéral du promontoire et la plateforme osseuse qui constitue le bord postérieur du foramen ovale. Cette portion représente aussi probablement une partie de la lame antérieure du pétromastoïde. Sur la face latérale de l'os, on observe un sillon profond et large qui recevait le sinus prootique; à son extrémité ventrale, un petit foramen correspond au débouché latéral du canal prootique.

Source : MNHN, Paris

DISCUSSION

La comparaison des crânes de *Pucadelphys* est problématique du fait de l'absence de crânes de marsupiaux fossiles du Tertiaire ancien ou du Crétacé qui soient raisonnablement bien connus. *Asiatherium* du Crétacé supérieur de Mongolie (SZALAY, 1993) est probablement un marsupial mais sa description détaillée est en cours et, de surcroît, cette espèce est loin de faire l'unanimité quant à son attribution aux métathériens. *Mayulestes ferox* MUIZON (1994) du même âge et du même gisement que *Pucadelphys*, est connu par un crâne remarquablement complet mais sa description détaillée est en cours. En revanche il existe de nombreux restes dentaires de marsupiaux dans le Crétacé supérieur d'Amérique du Nord et dans le Paléocène d'Amérique du Sud. La discussion comprendra donc une première partie qui comparera les dents de *Pucadelphys* aux formes voisines d'Amériques du Nord et du Sud, et une seconde partie qui passera en revue les principaux caractères crâniens de *Pucadelphys* afin d'en déterminer la polarité et qui tentera d'analyser les modalités de l'évolution du crâne chez les Theria et plus précisément chez les Tribosphenida.

COMPARAISON DENTAIRE. — Parmi les Didelphidae fossiles d'Amérique du Sud, *Sternbergia itaboraiensis* du Paléocène "moyen" d'Itaboraí (Brésil) est l'espèce qui se rapproche le plus de *Pucadelphys andinus* par la taille et la structure de ses dents à tel point que la première constitue un ancêtre morphologique idéal pour la seconde. *Pucadelphys* et *Sternbergia*, en plus de leur structure dentaire presque identique, possèdent la même morphologie du protocône renflé postérieurement, et le même important développement des styles B et C. Les molaires de *Sternbergia* diffèrent toutefois de celles de *Pucadelphys* par leur bassin du trigone, moins profond, leur paracône, plus réduit, leur centrocrista formant un V plus marqué, leur plateforme stylaire, plus petite, leur talonide, plus large, leur trigonide, plus bas, leur hypoconulide et entoconide, plus grands et par la présence d'un cingulum labial.

Deux autres Didelphidae d'Itaboraí présentent d'importantes ressemblances structurales avec *Pucadelphys*; ce sont : *Marmosopsis juradoi* et *Itaboraidelphys camposi*. Bien que dans ces cas la ressemblance ne soit pas aussi frappante que pour *Sternbergia*, *Pucadelphys* pourrait également représenter un bon ancêtre morphologique pour ces deux genres.

Pucadelphys montre également d'intéressantes ressemblances avec plusieurs espèces *d'Alphadon* et de *Protalphadon* d'Amérique du Nord, genres classés parmi les Peradectidae par MARSHALL *et al.* (1989). Les trois genres présentent des structures dentaires similaires mais *Pucadelphys* diffère des deux formes nord-américaines par la possession d'une centrocrista en V, d'un paracône plus petit que le métacône (ils sont sub-égaux chez *Alphadon* et *Protalphadon*) et d'un protocône à flanc postérieur renflé, trois caractères de Didelphidae. En fait, *Alphadon marshi* représente un bon ancêtre structural pour les Didelphidae (CLEMENS, 1966) et donc pour *Pucadelphys*. Cette interprétation confirme l'hypothèse de CLEMENS (1966) et de CROCHET (1980) qui pensent que les Didelphidae pourraient avoir leur origine parmi les Peradectidae nord-américains. Il est d'ailleurs intéressant de constater que certains spécimens d'*Alphadon marshi* ont une centrocrista en V et un paracône plus petit que le métacône (CIFELLI, 1990 : 315).

ANALYSE DE CARACTÈRES. — Sont passés en revue et discutés ci-dessous les états de caractères qui paraissent importants pour la compréhension de l'évolution des mammifères. Ils seront présentés dans l'ordre suivant : dentition, dentaire, os du crâne, foramens crâniens, et région auditive.

CARACTÈRES DENTAIRES

Nombre d'incisives. — *Pucadelphys* présente l'état plésiomorphe qui est la possession de 5/4 incisives.

Structure des incisives supérieures. — *Pucadelphys* est plésiomorphe par la morphologie conique de ses incisives qui sont d'une hauteur subégale.

Structure des incisives inférieures. — Tous les Didelphidae actuels ont une i3 dont la racine est décalée en quinconce vers l'arrière. Cette disposition est absente chez *Pucadelphys* qui retient donc l'état plésiomorphe pour ce caractère.

Nombre de molaires et prémolaires. — *Pucadelphys* présente P3/3 et M4/4, ce qui constitue l'état plésiomorphe de ce caractère au sein des marsupiaux.

Structure des molaires et prémolaires. — Avec une centrocrista en V, un paracône plus petit que le métacône et un protocône renflé postérieurement, *Pucadelphys* est en parfait accord avec la structure dentaire observée chez les Didelphidae.

DENTAIRE

Processus angulaire infléchi. — *Pucadelphys*, qui possède une telle structure, présente l'état plésiomorphe de ce caractère au sein des Tribosphenida.

Sillon mylohyoïdien. — La présence d'un sillon mylohyoïdien chez *Pucadelphys* est une plésiomorphie au sein des mammifères.

Foramen mandibulaire labial. — L'absence de ce type de foramen chez *Pucadelphys* représente l'état apomorphe de ce caractère puisqu'il existe chez la plupart des mammifères primitifs comme *Kielantherium*, *Prokennalestes*, *Oetlestes*, et *Zalambdalestes*. Sa présence chez *Microbiotherium gallegoense*, un Microbiotheriidae du Miocène inférieur d'Argentine, constitue probablement une réversion.

Source : MNHN, Paris

OS DU CRÂNE

Orbite grande et confluente avec la fosse temporale. — *Pucadelphys*, qui présente la condition observée sur tous les crânes de thériens du Crétacé, est plésiomorphe pour ce caractère.

Lacrimal. — Un lacrimal possédant une grande aile faciale est un état plésiomorphe présent chez *Pucadelphys*.

Contact nasal-lacrimal. — Un contact maxillaire-frontal est l'état plésiomorphe de ce caractère qui se rencontre chez les cynodontes, les tritylodontes, les multituberculés, *Morganucodon*, *Vincelestes*, et *Deltatheridium*. Il existe également chez les Borhyaenoidea (probablement un état plésiomorphe) et chez le vombatoïde *Wynyardia* (probablement une réversion). *Pucadelphys*, avec un net contact nasal-lacrimal, présente donc l'état dérivé de ce caractère.

Contact alisphénoïde-pariétal. — *Pucadelphys* présente un large contact entre l'alisphénoïde et le pariétal, ce qui constitue l'état plésiomorphe de ce caractère.

Fosses palatines. — L'absence de fosses palatines chez *Pucadelphys* est un état plésiomorphe qui existe également chez les cynodontes, les monotrèmes, les multituberculés, *Vincelestes*, *Deltatheridium*, et chez de nombreux métathériens.

Processus préglénoïde du frontal. — Cette plésiomorphie probable des Tribosphenida est présente chez *Pucadelphys*.

FORAMENS DU CRÂNE

Canal transverse. — Cette structure est absente chez *Morganucodon*, les monotrèmes, les multituberculés, les Deltatheroida, les Borhyaenoidea, certains Didelphidae, certains Dasyuridae et *Pucadelphys*, et constitue l'état plésiomorphe au sein des mammifères. Un canal transverse est présent chez tous les autres marsupiaux.

Foramen ovale. — Le terme de foramen ovale est ici utilisé pour désigner le passage de la branche mandibulaire du trijumeau (V3) indépendamment des os qu'il traverse. Le terme de foramen pseudovale utilisé par plusieurs auteurs (MacIntyre, 1967; Archer, 1976a) est extrêmement confus car souvent utilisé avec des sens différents.

Foramen subsquamosal. — La présence de ce foramen chez *Pucadelphys* est un état plésiomorphe retrouvé chez tous les métathériens et chez les euthériens crétacés, *Asioryctes* et *Kennalestes*.

Foramen postzygomatique. — La présence de ce foramen chez *Pucadelphys* est une plésiomorphie qui se retrouve chez tous les marsupiaux.

RÉGION AUDITIVE

Bulle tympanique ossifiée. — *Pucadelphys* ne possède pas de processus tympanique de l'alisphénoïde. L'absence de bulle tympanique ossifiée représente apparemment l'état plésiomorphe chez les mammifères (Novacek, 1977). L'absence de processus tympanique de l'alisphénoïde est une plésiomorphie chez *Pucadelphys* (et non une réversion, comme cela fut supposé par Marshall & Kielan-Jaworowska, 1992) et l'étude du crâne de *Mayulestes*, qui ne possède pas non plus de processus tympanique de l'alisphénoïde, suggère que ce caractère est apparu plusieurs fois au cours de l'évolution des marsupiaux (Muizon, 1994).

Orientation de l'ectotympanique et de la membrane tympanique. — Les avis divergent sur la position primitive de l'ectotympanique. Pour Novacek (1977), la position primitive est subhorizontale car cette disposition est présente chez les monotrèmes et chez *Lambdopsalis* et parce que l'ectotympnique est subhorizontal dans les stades précoces du développement ontogénique de tous les mammifères. Pour Kielan-Jaworowska (1981) l'ectotympanique est primitivement orienté à 45° car c'est la position de l'angulaire (= ectotympanique) chez les cynodontes et chez *Morganucodon*. De plus, l'ectoympanique des euthériens *Asioryctes* et *Kennalestes*, qui fut retrouvé *in situ* sur certains spécimens, présente une position à 45° de l'horizontale. Bien que l'ectotympanique de *Pucadelphys* soit inconnu, la position de la fenêtre ovale laisse supposer qu'il avait une position subverticale comme chez tous les autres marsupiaux. Quel que soit l'état plésiomorphe de ce caractère, la condition de *Pucadelphys* serait donc dérivée.

Sinus auditif. — L'absence de sinus auditifs chez *Pucadelphys*, qui sont en général abondants et vastes chez la plupart des autres marsupiaux, est un état plésiomorphe au sein du groupe.

Contribution de la pars mastoidea à l'occiput. — Cet état, présent chez *Pucadelphys* ainsi que chez de nombreux autres mammifères, est apparemment une plésiomorphie pour les Tribosphenida.

Mastoïde et processus paroccipital. — L'absence de processus paroccipital et la petite taille du processus mastoïde, comme cela se rencontre chez *Pucadelphys*, représentent apparemment un état primitif pour les mammifères.

Forme de la fenêtre ovale et de la base du stapes. — Avec un rapport longueur/largeur de la fenêtre ovale de 1,4, *Pucadelphys* est voisin de la condition plésiomorphe pour les marsupiaux.

Artère stapédiale. — L'artère stapédiale est présente chez les embryons de tous les mammifères actuels mais seulement chez les adultes d'*Ornithorhynchus* et d'euthériens. Son parcours, marqué par un profond sillon sur le promontoire, a été mis en évidence chez les multituberculés et chez de nombreux euthériens fossiles. L'artère stapédiale disparaît chez les marsupiaux adultes, lesquels ne présentent pas de sillon sur le promontoire et sont caractérisés par cette synapomorphie. La présence d'une artère stapédiale chez l'adulte est une plésiomorphie chez les mammifères et l'absence de sillon du promontoire (perte de l'artère stapédiale) chez *Pucadelphys* serait indicateur d'un état apomorphe au sein des mammifères mais plésiomorphe au sein des marsupiaux.

Source : MNHN, Paris

Cours de la carotide interne. — Le cours de ce vaisseau chez *Pucadelphys* est situé sur le bord médial du promontoire. Cette disposition est également présente chez tous les autres marsupiaux, chez les monotrèmes, chez les euthériens du Crétacé supérieur d'Asie et chez certains euthériens actuels (rongeurs, lagomorphes, ongulés) et constitue l'état plésiomorphe (PRESLEY, 1979). L'état apomorphe, où la carotide interne est latérale au promontoire, existe chez tous les autres euthériens et a dû apparaître plusieurs fois au cours de l'évolution. *Pucadelphys* retient donc l'état plésiomorphe pour ce caractère.

Sillon pour le nerf facial. — La présence d'un sillon pour le nerf facial, chez *Pucadelphys*, est une plésiomorphie au sein des mammifères.

Sinus et foramen pétreux inférieurs. — La présence de ces structures chez *Pucadelphys* constitue une plésiomorphie au sein des mammifères.

Lame antérieure. — Le pétromastoïde de *Pucadelphys* possède une lame antéro-latérale qui participe à la formation de la paroi interne de la boîte crânienne. À la hauteur de cette lame, la paroi externe du crâne est formée par l'alisphénoïde et le squamosal. Médialement cette lame possède une fosse qui recevait très probablement le ganglion trigéminé. Chez des mammifères primitifs comme *Morganucodon*, *Haldanodon*, les multituberculés, *Vincelestes* et les monotrèmes, le pétromastoïde présente une grande lame antérieure qui participe seule à la formation de la paroi latérale du crâne. Elle s'articule antérieurement avec le bord postérieur de l'alisphénoïde et sa face médiale présente une fosse qui recevait le ganglion trigéminé. Chez les marsupiaux et les placentaires actuels, il n'existe pas de lame antérieure du pétromastoïde et, seul, l'alisphénoïde participe à la construction de la paroi latérale du crâne. WIBLE (1990) a cependant noté qu'il existait parfois chez certains marsupiaux, une structure extrêmement réduite qui pourrait représenter une relique de la lame antérieure des mammifères primitifs. La structure laminaire observée chez *Pucadelphys*, laquelle possède sur sa face médiale la même fosse pour le ganglion trigéminé que celle observée chez les mammifères non-tribosphéniques cités plus haut et qui occupe la même position que chez ces formes, est ici considérée comme homologue de la lame antérieure. La présence chez *Pucadelphys* d'une lame antérieure encore bien développée, quoique nettement plus réduite que chez les mammifères non tribosphéniques, semble démontrer que la réduction et la disparition de la lame antérieure du pétromastoïde est une synapomorphie des Tribosphenida, comme l'avait mentionné WIBLE (1990). *Pucadelphys* représente une étape intermédiaire dans cette réduction; chez ce genre, la lame antérieure est expulsée de la face externe de la paroi latérale du crâne par l'apparition d'une articulation du squamosal avec l'alisphénoïde mais reste toujours présente, bien que réduite, sur la face interne de la paroi latérale du crâne. A ce stade, la paroi latérale du crâne, dans la région antérieure du pétromastoïde, est donc une double lame dont la portion latérale est formée par le squamosal et l'alisphénoïde et la portion médiale par la lame antérieure du pétromastoïde. Le stade suivant (marsupiaux et placentaires actuels) voit la disparition de la lame antérieure. *Pucadelphys* est donc la démonstration paléontologique de la polarité d'un caractère important de l'évolution de la paroi crânienne des mammifères et confirme les hypothèses de WIBLE (1990) et de HOPSON & ROUGIER (1993).

CONCLUSIONS

Le crâne de *Pucadelphys* représente un cas classique d'évolution en mosaïque. *Pucadelphys* possède de nombreux caractères plésiomorphes de marsupiaux, de Tribosphenida, de thériens et de Mammifères. Il possède néanmoins des caractères apomorphes qui tendent à le rapprocher de la famille des Didelphidae. La présence d'une lame antérieure du pétromastoïde est un caractère plésiomorphe pour un marsupial qui tendrait à en faire le groupe frère de tous les autres marsupiaux et donc à le placer dans un taxon nouveau; en fait *Pucadelphys* présente déjà l'apomorphie des Tribosphenida consistant en une réduction de la lame antérieure du pétromastoïde, une structure qui a pu disparaître plusieurs fois au cours de l'évolution de ce groupe. L'absence de processus tympanique de l'alisphénoïde (structure longtemps considérée comme une synapomorphie des marsupiaux) tendrait également à en faire le groupe frère plésiomorphe pour ce caractère de tous les autres marsupiaux ou à envisager une réversion. En fait, l'étude de *Mayulestes ferox*, un borhyaenoïde du même gisement que *Pucadelphys* et ne possédant pas de processus tympanique de l'alisphénoïde, a montré que cette structure était sans doute apparue plusieurs fois au cours de l'évolution des marsupiaux et ne constitue pas un obstacle à la classification de *Pucadelphys* parmi les Didelphidae.

Les seuls caractères dérivés, au sein des marsupiaux, que possède *Pucadelphys* sont ceux de la structure de ses molaires supérieures qui le rangent sans équivoque au sein des Didelphidae.

Source : MNHN, Paris

INTRODUCTION

Skulls and basicranial bones of mammals are very important in phylogenetic studies, yet these elements are extremely rare in rocks of Cretaceous and earliest Paleocene Age. Because of a dearth of such specimens, little is known of the early cranial evolution of Tribosphenida (metatherians, eutherians and their common ancestors with tribosphenic dentitions; *sensu* McKenna, 1975). In fact, the character states of skull features in the direct common ancestor of metatherians and eutherians are unknown, yet inferences about these states have been made based on study of a few late Cretaceous specimens and of Cenozoic and living taxa (Kemp, 1982; 1983).

To date, there are only two non-tribosphenid therians for which cranial material is known. One is a eupantothere from the late Jurassic of Portugal, *Henkelotherium guimarotae* which is represented by a very partial skull associated with a nearly complete skeleton (Henkel & Krebs, 1977; Krebs, 1987; Krebs, 1991), and the other is the eupantothere *Vincelestes neuquenianus* from the early Cretaceous of Argentina, which is known from nearly complete skulls and skeletons which have not yet been fully described (Bonaparte & Rougier, 1987; Rougier & Bonaparte, 1988; Rougier *et al.*, 1992; Hopson & Rougier, 1993).

Eutherians are the best known of late Cretaceous tribosphenids, and complete or partial skulls of *Asioryctes*, *Barunlestes*, *Kennalestes* and *Zalambdalestes* have been described from the ?late Santonian and/or Campanian of Asia (Kielan-Jaworowska, 1981; 1984; Kielan-Jaworowska & Trofimov, 1980).

In sharp contrast, basicranial remains of metatherians from the late Cretaceous are extremely rare. Deltatheroida, the possible plesiomorphic sister-group of marsupials (Kielan-Jaworowska & Nessov, 1990; Marshall & Kielan-Jaworowska, 1992) are known by several partial skulls and by one almost complete skull (e.g. Anonymous, 1983), although the basicranial region has not been described. Specimens of metatherians which have been described include a right ventrolateral corner of a skull of *Eodelphis browni* (Stagodontidae) from the Belly River Formation of Alberta (Matthew, 1916); a left ventrolateral corner of a skull of *Didelphodon vorax* (Stagodontidae) from the Lance Formation of Wyoming (Clemens, 1966; a second ear region described by Clemens as *D. vorax* is a multituberculate; see Wible, 1990); a nearly complete left petromastoid from the Hell Creek Formation of Montana which Archibald (1979) described as either *Pediomys hatcheri*, *P. florencae* or *Alphadon rhaister* but which Wible (1990) calls Petrosal Type D (possibly *A. rhaister*); and ten petromastoids from the late Cretaceous of North America which Wible (1990) refers to as Petrosal Type A (one specimen, probably *Pediomys hatcheri* or *P. florencae*), B (one specimen, possibly *P. hatcheri* or *P. florencae*), and C (eight specimens, indeterminate). Recently Trofimov & Szalay (1993) gave a short presentation of a new marsupial from the late Cretaceous of Mongolia. The specimen is an almost complete skeleton of a *Monodelphis scalops* -sized animal which has a marsupial dental formula and marsupial features in its dental morphology. In the early Paleocene of the Santa Lucía Formation (Bolivia) another specimen of early Metatheria is a partial skeleton of a new borhyaenoid, *Mayulestes ferox*, Muizon, 1994, which includes a very complete skull. As mentioned in its preliminary description, the skull of *Mayulestes* bears several features that question the traditional definition of Metatherians.

Source : MNHN, Paris

In this part of the volume we describe nearly complete skulls of the metatherian *Pucadelphys andinus* MARSHALL & MUIZON (1988) from the early Paleocene age Santa Lucía Formation (*sensu* GAYET *et al.*, 1992) at Tiupampa in southcentral Bolivia (Fig. 1). With a nearly complete undescribed skull of a deltatheroid from the late Cretaceous of Asia (ANONYMOUS, 1983; KIELAN-JAWOROWSKA & NESSOV, 1990), the marsupial skeleton mentioned above (TROFIMOV & SZALAY, 1993), and the skeleton of *Mayulestes*, these are among the earliest complete skulls of metatherians (or possible metatherians) yet known. As shown below, these skulls reveal numerous character states which have important bearing on the phylogenetics of Metatheria, in particular, and on Tribosphenida, in general. The postcranial skeleton is described in the part III of this volume (MARSHALL & SIGOGNEAU-RUSSELL, 1995).

ABBREVATIONS OF INSTITUTIONS. — MNHN, Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris; YPFB Pal, paleontology collection of Yacimientos Petrolíferos Fiscales de Bolivia in the Centro de Tecnología Petrolera, Santa Cruz, Bolivia.

SYSTEMATIC PALEONTOLOGY

Serial designation for teeth follows LUCKETT (1992) contra ARCHER (1978), HERSHKOVITZ (1982), MARSHALL & MUIZON (1988) and MUIZON (1992) (i.e. premolars are P1, P2, P3; deciduous tooth is dP3; permanent molars are M1, M2, M3, M4); terminology for molar structure is shown in Figure 5; usage of Metatheria follows MARSHALL *et al.* (1989), [although we admit that the Deltatheroida could possibly be included in this taxon as recommended by KIELAN-JAWOROWSKA & NESSOV (1990) and MARSHALL & KIELAN-JAWOROWSKA (1992); usage of Theria follows KIELAN-JAWOROWSKA *et al.* (1987), and Tribosphenida follows MCKENNA (1975); suprageneric ranks of Metatheria follows MARSHALL *et al.* (1989). All measurements are in millimeters (mm). Abbreviations of teeth are as follows: c, lower canine; C, upper canine; i, lower incisor; I, upper incisor; m, lower molar; M, upper molar; p, lower premolar; P, upper premolar.

Legion TRIBOSPHENIDA McKenna, 1975
Infraclass METATHERIA Huxley, 1880
Order DIDELPHIMORPHIA (Gill, 1872) Marshall *et al.*, 1989
Family DIDELPHIDAE Gray, 1821
Genus *PUCADELPHYS* Marshall & Muizon, 1988

TYPE-SPECIES. — *Pucadelphys andinus* MARSHALL & MUIZON, 1988
DIAGNOSIS. — Same as for type and only known species.

Source : MNHN, Paris

Pucadelphys andinus MARSHALL & MUIZON, 1988

HOLOTYPE. — YPFB Pal 6105, a nearly complete skull (missing part of left zygomatic arch) and associated dentaries with alveoli of I2-5, and I1 and C1-M4 present on right side; alveoli of I1 and I3-5, crowns of I2 and C1, roots of P1, P2 missing, posterior half of P3, and M1-4 present on left side; right dentary missing ventromedial edge of horizontal ramus with alveoli of i1 and i4, root of i2, complete i3, complete c1-m4 (p3 not fully erupted); posterior part of left dentary

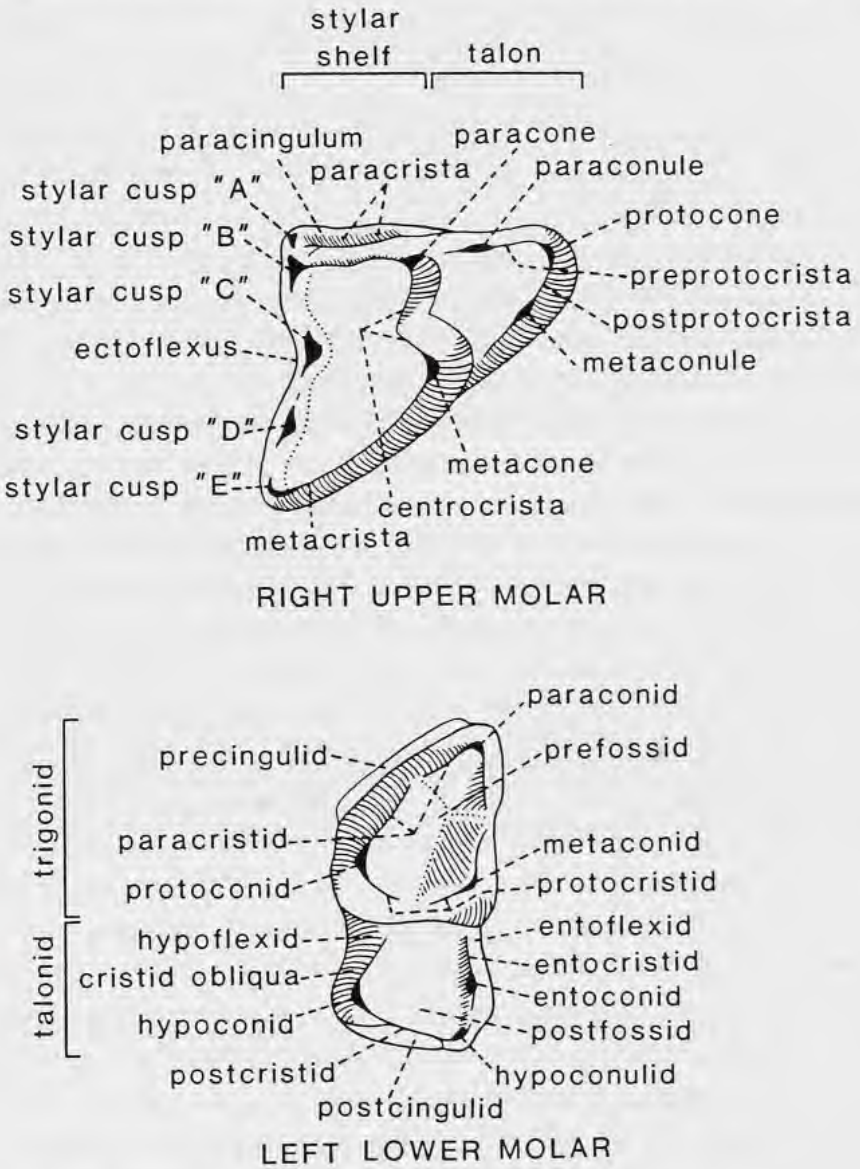

FIG. 5. — Terminology for molar structure of a generalized marsupial (after MARSHALL, 1987).

FIG. 5. — *Terminologie de la structure des molaires d'un marsupial primitif (d'après MARSHALL, 1987).*

Source : MNHN, Paris

with m1-4; and associated articulated partial skeleton of neck and thoracic regions (figured by MARSHALL & MUIZON, 1988, Figs 1, 3A).

HYPODIGM. — The holotype, YPFB Pal 6105; YPFB Pal 6107, greater part of skull and articulated dentaries with root of right C1 and complete right P1-M4 and p2- m4, complete left C1-M4 and c1-m4, and palatal and basicranial part of skull crushed slightly internally; YPFB Pal 6108, greater part of dorsoventrally crushed skull with associated dentaries, with complete C1-M4, alveoli of i1-4 and c1-m4 present (missing tips of p3 and m3 protoconid) on right side, and root of C1, complete P1-M4, root of c1, alveoli of p1, p2-3 present (missing all but bases of crowns) and m2-4 present (m2 missing tips of para-and metaconid, m4 missing tip of paraconid) on left side; YPFB Pal 6109, rostral part of skull with right C1-P3 and trigon of M2, left P1-M4 (figured by MARSHALL & MUIZON, 1988, fig. 3B), greater part of left dentary with bases of c1 and p1, and p2-m4 complete (figured by MARSHALL & MUIZON, 1988, fig. 3C); YPFB Pal 6110, greater part of skull and articulated dentaries with most of dentition (missing only I1-5, left P1 and tip of left p2) and part of articulated thoracic region of skeleton (figured by MARSHALL & MUIZON, 1988, fig. 2); YPFB Pal 6470, anterior part of skull (dorsoventrally crushed) with left I2 complete, alveoli of I1 and I3-5, complete C1-M4, right C1-M4 complete, basicranium with complete right petromastoid and four articulated vertebrae, anterior half of right dentary with c1 and p2-m2 complete, and alveoli of p1, and greater part of left dentary with i1 complete, alveoli of i2-4, c1 complete, roots of p1, and p2-m4 present (trigonid of m4 missing); YPFB Pal 6471, premaxilla with right C1-P1, fragment of left maxilla with M2-4 complete and attached zygomatic arch with glenoid fossa, exoccipital region of skull with three articulated vertebrae, anterior ends of left and right dentaries with c1-p1 in each, and posterior part of left dentary with m3-4; YPFB Pal 6472, right maxilla and premaxilla with complete C1-M4, complete right dentary with bases of i1-4, and complete c1-m4; YPFB Pal 6473, left maxilla with complete M1-4, greater part of left dentary with root of i1, base of i2, complete i3-4, c1 missing tip of crown, and virtually complete p1-m4; YPFB Pal 6474, greater part of left dentary of juvenile with three incisors and alveolus of a fourth, c1 erupting, p2 and m2 complete, and trigonid of erupting m3; YPFB Pal 6475, right maxilla with M1-4 (M2 missing anterolabial corner of crown); YPFB Pal 6476, right maxilla with M2-4; YPFB Pal 6477, right maxilla with M2-3 and parastyle of M4; YPFB Pal 6478, right maxilla with M2-3; YPFB Pal 6479, anterior part of right dentary with c1-p3 complete and broken base of m1; YPFB Pal 6480, fragment of a right dentary with posterior half of p3, complete m1, and trigonid of m2; YPFB Pal 6481, fragment of right dentary with m3-4 (trigonids broken on both); YPFB Pal 6482, fragment of right dentary with m1 missing trigonid and complete m2; YPFB Pal 6483 (=MNHN Vil 118), an isolated left m2 missing tip of paraconid (figured by MUIZON *et al.*, 1984, fig. 8); YPFB Pal 6484 (=MNHN Vil 127), an isolated left m4 missing tip of metaconid and posterior edge of entoconid (figured by MUIZON *et al.*, 1984, fig. 9); YPFB Pal 6485, fragment of left maxilla with broken roots of C1-P1 and complete P2-M4.

Source : MNHN, Paris

HORIZON AND LOCALITY. — The specimens of *Pucadelphys andinus* described here were recovered from the Santa Lucía Formation (*sensu* GAYET *et al.*, 1992) at Tiupampa, located about 95 km southeast of Cochabamba (see MARSHALL *et al.*, part I of this volume).

AGE. — Tiupampan Land Mammal Age (*sensu* ORTIZ JAUREGUIZAR & PASCUAL, 1989; MARSHALL, 1989), early Paleocene (VAN VALEN, 1988; GAYET *et al.*, 1992; BONAPARTE *et al.*, 1993; MUIZON & BRITO, 1993; MARSHALL *et al.*, part I of this volume).

DIAGNOSIS (skull morphology only). — I5/4 C1/1 P3/3 M4/4; I1-5 in continuous series (no diastem); i3 not staggered; cheek teeth structure as in Didelphidae: paracone smaller in size in occlusal view and distinctly lower in lateral view than metacone; centrocrista V-shaped with apex of V pointing labially toward stylar cusp C; stylar shelf well developed; stylar cusp B highest of stylar cusps; stylar cusps A, C and D subequal in size and only slightly smaller than stylar cusp B; parastyle spur-like, extends anteriorly and overhangs posterolabial edge of preceding tooth; remnant of mylohyoid groove; large medially inflected angular process; rostrum short; secondary palate solid (no evidence of vacuities) and extends posteriorly to point behind M4; nasals narrow anteriorly, much expanded posteriorly with W-shaped contact with frontals; small frontal-maxilla contact; lacrimal with large facial wing; lacrimal canal large, opens within orbit; orbit confluent with temporal fossa; jugal participates in formation of preglenoid process; glenoid fossa situated posteriorly opposite anterior half of promontorium; subsquamosal foramen present; tympanic area uncovered, no evidence of ossified auditory bulla or of ossified ectotympanic; tympanic membrane apparently oriented obliquely at 45° or more from horizontal; no auditory sinuses; promontorium large, teardrop-shaped, inflated ventrally; sulci for facial nerve, sigmoid sinus, inferior petrosal sinus, prootic sinus, and sphenoparietal emissary vein; internal carotid artery medial in position; no evidence of transverse canal; prootic canal for lateral head vein (vena capitis lateralis) present; petromastoid with anteroanterior laminar structure which is regarded here as homologous to the anterior lamina of the non-tribosphenid mammals; foramen ovale (exit for V3) located posteriorly opposite anterior part of glenoid fossa, rimmed anteriorly by alisphenoid and posteriorly by anterior lamina of petromastoid; external acoustic meatus very small.

DESCRIPTION

Anatomical features are described in the following order: upper dentition, lower dentition, dentary and skull .

I1-5 (Figs 10 and 12). — The right I1 is preserved in YPFB Pal 6105 and the left I2 in YPFB Pal 6470; both teeth have small rounded crowns. As shown by the alveoli of I1-5 preserved on the right and left side of YPFB Pal 6105 and left side of YPFB Pal 6470, a slight size increase occurs from I1 to I4 (I3 and I4 are subequal in size) and I5 is smaller than I4, being similar in size to I1. The edges of the alveoli of I1-4 are on the same level, while that of I5 is situated more dorsally in the anteriormost edge of a large fossa in the posterior part of the premaxilla which accomodates

Source : MNHN, Paris

the tip of c1. I1-5 occur in a continuous sequence with no spaces between them or between the left and right I1's. A distinct diastema (1.4 mm on left side of YPFB Pal 6105) separates I5 from C1.

C1 (Figs 10 and 12). —This tooth is large, pointed and arcs ventroposteriorly such that the tip of the crown is about ventral to the posterior edge of the crown base. In cross section C1 is ovoid, being longer than wide (2.2 mm x 1.2 mm at the base of right C1 in YPFB Pal 6105). C1 is consistently larger than c1 in specimens where both are preserved. C1 is either in direct contact with P1 or separated from it by a very small diastema.

P1-3 (Figs 6 and 7). — These three teeth are all double-rooted; an increase in crown length, width and height occurs from P1 to P3. P1 is considerably smaller than P2-3 (Table 1); in occlusal view it is ovoid, a low ill-defined heel occurs posterobasally, and the crown tip lies ventral to the posterior edge of the anterior root. P2 is slightly smaller than P3 (Table 1); the crown tip lies ventral to the anterior edge of the posterior root, at about the same height as the occlusal surfaces of M1-4. A distinct cusp occurs posterobasally and a very small cuspule occurs anterobasally. Weak basal cingula usually occur along labial and lingual edges of crown posteriorly, and there is a distinct posterolingual swelling of the crown. P3 is the largest of upper premolars; the crown tip lies medially below the center of the tooth and is considerably higher than the occlusal surfaces of M1-4. There is a distinct posterobasal cusp, an anterobasal cuspule (which is larger than that on P2), a distinct posterobasal cingulum labially, and a weaker basal cingulum lingually which extends from the anterobasal cuspule to the posterobasal cusp.

M1-4 (Figs 6 and 7). — In average length M1≈M2>M3>M4 and in average width M1<M2<M3>M4 (Table 1). The protocone is large, broad anteroposteriorly, and inflated basally, particularly posterolingually. The preprotocrista is slightly shorter and more rectilinear than the postprotocrista which has a distinct posterolingual bow on M1-3. The trigon is distinctly basined on M1-3, less so on M4. The para- and metacone are well developed on M1-3. The paracone is slightly smaller in occlusal view and lower in lateral view than the larger and higher metacone on M1-3 (on M4 the paracone is very large and high and the metacone, very reduced to absent). The metaconule is slightly larger than the paraconule on M2-3, subequal on M1. The centrocrista is V-shaped (dilambdodont; sensu CROCHET, 1980) with apex of V pointing labially toward stylar cusp C. The para- and metacone are weakly V-shaped (not connate) with their apex pointing lingually toward the para- and metaconule, respectively. The paracone, the centrocrista and the metacone form a weak W-shaped structure in occlusal view. The paracrista is low, short, rectilinear, and unites the paracone with a large stylar cusp B on M1-4. The metacrista is low, slightly longer than the paracrista on M1-3 (particularly on M1-2) and with a posterior bow (on M2-M3). The stylar shelf is well developed on M1-3 with an anteroposteriorly elongate basin separating para- and metacone from the row of large stylar cups. The stylar cusp B is the largest of stylar cusps; the stylar cusps A, C and D are also well developed, subequal in size and only slightly smaller than the stylar cusp B on M1-2. On M3 the stylar cusp A is subequal to B, while C and D are more reduced; on M4 stylar cusps A and B are fused into a large parastyle (other stylar cusps are extremely reduced or absent). There is no distinct evidence of a stylar cusp E on M1-4. A prominent parastyle, formed by spur-like stylar cusps A and B, extends anteriorly and

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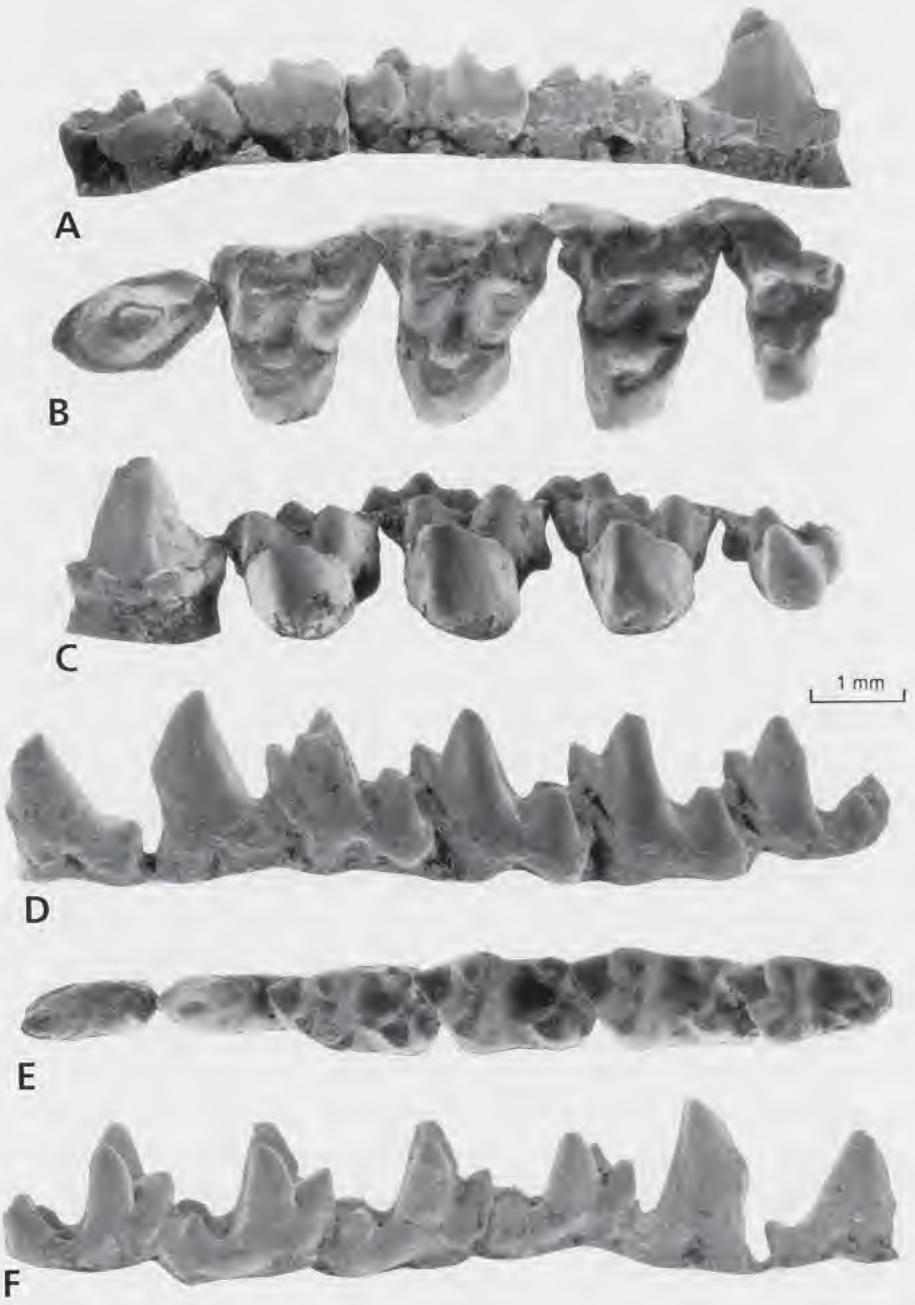

FIG. 6. — *Pucadelphys andinus*. SEM photos of left P3-M4 (A, labial; B, occlusal; C, lingual views) of YPFB Pal 6470; and left p2-m4 (D, labial; E, occlusal; F, lingual views) of YPFB Pal 6109. X 15.

FIG. 6. — Pucadelphys andinus. *Photos MEB de P3-M4 gauches (A, vue labiale; B, vue occlusale; C, vue linguale) d'YPFB Pal 6470; et p2-m4 gauches (D, vue labiale; E, vue occlusale; F, vue linguale) d'YPFB Pal 6109. X 15.*

Source : MNHN, Paris

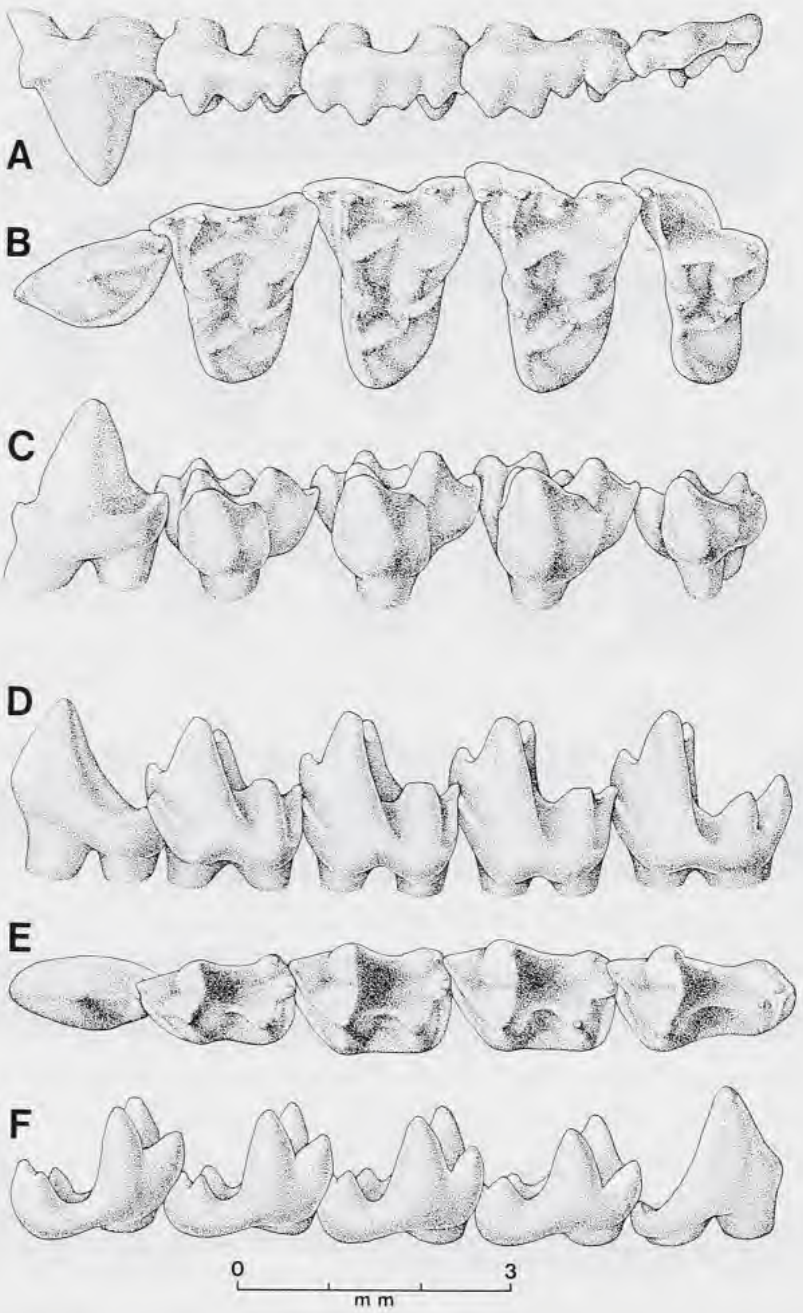

FIG. 7.—*Pucadelphys andinus*. A-C, left P3-M4 (A, labial; B, occlusal; C, lingual views), based on YPFB Pal 6109 and 6470; D-F, left p3-m4 (D, labial; E, occlusal; F, lingual views), based on YPFB Pal 6109 and 6473.

FIG. 7.—Pucadelphys andinus. *A-C, P3-M4 gauches (A, vue labiale; B, vue occlusale; C, vue linguale), d'après YPFB Pal 6109 et 6470; D-F, p3-m4 gauches (D, vue labiale; E, vue occlusale; F, vue linguale), d'après YPFB Pal 6109 et 6473.*

Source : MNHN, Paris

overlaps the posterolabial edge (i.e. metastylar region) of the preceding tooth. A distinct paracingulum extends along anterolabial edge of crown from stylar cusp A; it becomes very narrow below the tip of the paracone (it disappears on M4) and continues lingually to disappear below the paraconule. The ectoflexus is absent or very shallow on M1 and increases in depth from M1 to M3. M2 differs from M1 in being slightly wider, having a slightly deeper ectoflexus, and a longer paracrista relative to metacrista. M3 differs from M1-2 in having a distinct ectoflexus, an enormous spur-like parastyle on which stylar cusps A and B are large and subequal in size, smaller stylar cusps C and D, a metastyle area reduced in size relative to the more prominent parastyle area, para- and metacrista more subequal in length, and a crown less bulbous and narrower anteroposteriorly (i.e. more transversely elongate).

i1-4 (Fig. 8). — A left i1 is preserved in YPFB Pal 6470, a right i3 in YPFB Pal 6105, a right i4 in YPFB Pal 6472, and left i3-4 in YPFB Pal 6473. The i1-4 have simple ovoid crowns and increase slightly in size from i1 to i4; i4 is in direct contact with c1.

c1 (Fig. 8). — This tooth is large, pointed, arcs in anterodorsal direction. It is ovoid in cross-section, longer than wide (1.5 mm x 1.0 mm in right YPFB Pal 6105). The axis of the tooth is set at a slight oblique angle relative to the cheek tooth series (i.e. anterior edge labial, posterior edge more lingual). c1 is consistently smaller than C1.

p1-3 (Figs 6 and 7). — All three teeth are two-rooted. p1 is very small relative to p2-3, and is separated from c1 and p2 by small (0.5 mm) diastems. It is ovoid in occlusal view with the highest point of the crown set above the anterior edge of the anterior root. p2-3 are subequal in length and width (Table 1) although p2 tends to be slightly lower in height; both are distinctly premolariform with well developed posterobasal heels. The crown tips are about same level as protoconid tips of m1-4. The p2 differs from p3 in having the principal cusp narrower anteroposteriorly and inclined more anteriorly so that the tip occurs above the middle of the anterior root (on p3 the anteroposteriorly broader primary cusp is more dorsally directed so that tip occurs dorsal to posterior edge of anterior root); p2-3 occur in close succession without spaces separating them or p3 from m1.

m1-4 (Figs 6 and 7). — In average length m1<m2≈m3>m4, in average width m1<m2≈m3>m4 (Table 1). The labial side of teeth is higher than the lingual side, and the trigonid is well elevated above the talonid. The trigonid of m1 is relatively long (paraconid set anterolabially), while those of m2-4 are foreshortened anteroposteriorly and distinctly wider than long (paraconid set more lingually). The protoconid is the highest of the trigonid cusps and slightly higher than the metaconid. The paraconid is smaller than the metaconid and inclined anteriorly. Protoconid and metaconid are united by a straight trenchant protocristid. The talonid is broad and distinctly basined on m1-4, being wider than the trigonid on m1-3, and narrower on m4. The hypoconid is the dominant talonid cusp on m1-3; it is V-shaped in appearance, and considerably larger than entoconid and hypoconulid in occlusal view. In lateral view of m1-3 all three talonid cups are subequal in height. A short cristid obliqua contacts the trigonid at the posteromedial surface of the protoconid, labial to the protocristid notch. The hypoflexid is well developed on m1-4. Entoconid and hypoconid are subequal in size in occlusal view on m1-3, and the hypoconulid is "twinned" with the entoconid (i.e. set closer to entoconid than to hypoconulid). On m4 entoconid and

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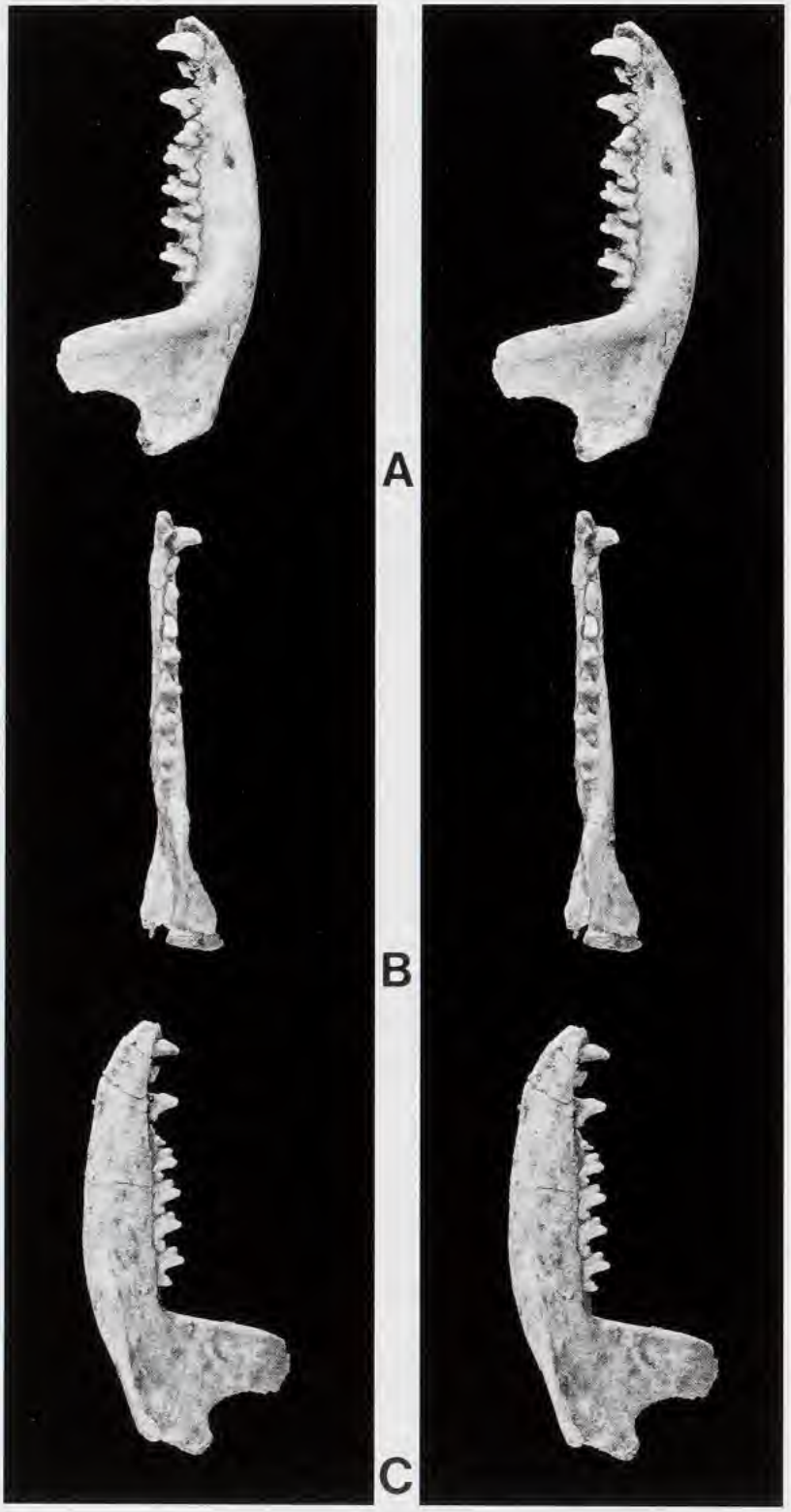

Source : MNHN, Paris

hypoconulid are fused basally, and the hypoconid is distinctly elevated above the much lower entoconid and hypoconid. A precingulid is well developed on m1-4; a postcingulid (i.e. shelf extending ventrolabially from tip of hypoconulid across posterior surface of hypoconid) is well developed on m1-3 but absent on m4.

DENTARY (Figs 8 and 9). — The horizontal ramus is long and slender. The ventral border of the bone is relatively flat between p1 and m3, bending dorsally anterior to p2 and posterior to m3. The deepest point occurs below m3-4, with a gentle decrease in depth from m3 to p1.

The articular surface of the symphysis is slightly rugose and covered by numerous vascular foramina; a well-developed symphyseal ligament was apparently present. The long axis of the symphyseal surface lies at an angle of about 40° to the horizontal axis of the dentary and extends posteriorly to below p2. There are typically two large mental foramina, one below p1 and another below m1. A groove on the medial surface of the dentary, about 1/3 of the way above the ventral edge, extends from the anterior edge of the angular process to below m1, becoming shallower anteriorly. This represents the mylohyoid groove (BENSLEY, 1902) and marks the course of a neurovascular bundle which probably included the mylohyoid artery and nerve. The angular process is very large and inflected medially; it is situated far posteriorly, more or less below the condyloid process. The mandibular foramen is situated dorsal to the anterior edge of the angular process and below the middle of the coronoid process. The masseteric fossa is shallow with a posteroventral border (between the condyloid process and the point directly ventral to the middle of the coronoid process) developed into a broad laterally directed shelf. In dorsal and ventral views, the posterior part of the dentary has a broad V-shape due to the large medially inflected angular process and the large laterally directed expansion of the posteroventral part of the masseteric border. The condyloid process is wide transversely; the portion projecting lateral to the vertical plane of the dentary is about three times longer (transversally) than that projecting medially. It occurs dorsal to the horizontal plane through m1-4, at about the same level as the tip of c1. Its articular surface is broadly convex dorsoposteriorly. The coronoid process of the ascending ramus is broad anteroposteriorly, thin transversely with the anteroposterior axis in the same vertical plane as the labial sides of m1-4. Its upper margin is rounded (convex dorsally) and its posterior border is markedly concave posteriorly.

GENERAL SKULL STRUCTURE (Figs 10 -14 and 16). — There are five partial or nearly complete skulls. The most complete and least distorted is the type YPFB Pal 6105 (Figs 10 and 18) which is the basis for the reconstructions in Figs 10, 15 and 17 along with details incorporated from other

FIG. 8. — *Pucadelphys andinus*. Right dentary of YPFB Pal 6108 (A, lateral; B, dorsal; C, medial views). Stereophotos X 2.5.

FIG. 8. — Pucadelphys andinus. *Dentaire droit d'YPFB Pal 6108 (A, vue latérale; B, vue dorsale; C, vue médiale). Photos stéréoscopiques X 2.5.*

Source : MNHN, Paris

specimens as indicated. In YPFB Pal 6105 the nasals and the left part of the rostrum anterior to the infraorbital canal are slightly crushed ventrally, but the remainder of the skull is virtually undistorted. Specimens YPFB Pal 6107 (Fig. 14) and 6110 (Fig. 13) are crushed slightly transversely, particularly in the basicranial and palatal areas. This crushing is most extreme in YPFB Pal 6110 where the basioccipital is missing, the exoccipitals are in near contact and the

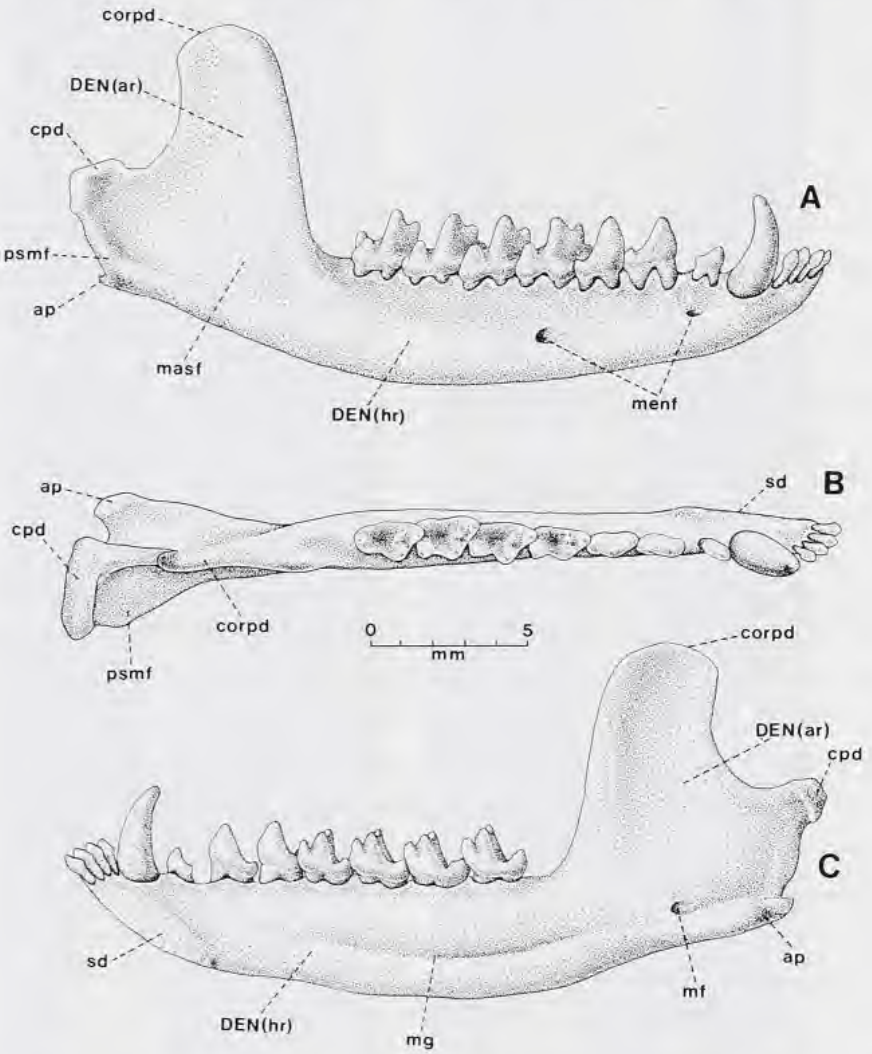

FIG. 9. — *Pucadelphys andinus*. Reconstruction of right dentary of YPFB Pal 6108 (A, lateral; B, dorsal; C, medial views). Abbreviations: **ap**, angular process of dentary; **corpd**, coronoid process of dentary; **cpd**, condyloid process of dentary; **DEN(ar)**, ascending ramus of dentary; **DEN(hr)**, horizontal ramus of dentary; **masf**, masseteric fossa; **menf**, mental foramen; **mf**, mandibular foramen (=inferior alveolar foramen); **mg**, mylohyoid groove (=meckelian groove); **psmf**, posterior shelf of masseteric fossa; **sd**, symphysis of dentary.

FIG. 9. — Pucadelphys andinus. *Reconstitution du dentaire droit d'YPFB Pal 6108 (A, vue latérale; B, vue dorsale; C, vue médiale). Abréviations:* ***ap****, processus angulaire du dentaire;* ***corpd****, processus coronoïde du dentaire;* ***cpd****, condyle articulaire du dentaire;* ***DEN(ar)****, branche ascendante du dentaire;* ***DEN(hr)****, branche horizontale du dentaire;* ***masf****, fosse massétérine;* ***menf****, foramen mentonnier;* ***mf****, foramen mandibulaire (= foramen alvéolaire inférieur);* ***mg****, sillon mylohyoïdien (= sillon de Meckel);* ***psmf****, plateforme postérieure de la fosse massétérine;* ***sd****, symphyse du dentaire.*

Source : MNHN, Paris

anterior ends of the pars petrosa of the petromastoids are in direct contact. The fourth skull, YPFB Pal 6108 (Fig. 16), is crushed dorsoventrally and the dorsal surface is displaced to the left relative to the ventral surface. The rostral portion of the fifth specimen, YPFB Pal 6109 (Fig. 11), shows virtually no distortion on the right side, although the nasals are slightly depressed anteriorly and the posterior part of the left maxilla is separated from the rest of the skull.

In YPFB Pal 6105 the ratio of the condylar-premaxilla length (28.5 mm) and the breadth between the outer edges of the zygomatic arches (approx. 19.5 mm) is about 0.68. The ratio betweenthe condylar-canine length (25.0 mm) and the broadest point of the braincase measured between the outer edges of the mastoid processes (11.0 mm) is 0.44.

The most distinct aspect of the skull in dorsal view is the short rostrum and overall bilobed appearance, with a broad area between the lacrimals and another between the posterior bases of the large zygomatic arches (Fig. 12). The narrowest point of the skull, excluding the nasal region, is just anterior to the frontal-parietal suture, the site of the interorbital constriction. The orbit is broadly confluent with the temporal fossa.

A weak sagittal crest occurs in all specimens, but is best developed in YPFB Pal 6105 where it begins on the posterior part of the frontals; in the other specimens the sagittal crest occurs only on the parietals and begins at the frontal-parietal suture. In all specimens the sagittal crest becomes higher and more prominent posteriorly. A dorsoposteriorly directed lambdoidal crest of the postparietal is well developed in all specimens. In ventral view (Fig. 12) the palate, including the dentition, and the basicranium are similar in size and shape, being broadly triangular with their apices directed anteriorly.

In lateral view (Fig. 12) the recess for the external acoustic meatus is small, broadly U-shaped, and bounded posteriorly by a small posttympanic process of the squamosal; it is situated immediately ventral to the subsquamosal foramen and dorsoposteriorly to the postglenoid foramen. The glenoid fossa is situated far posteriorly, opposite the anterior extremity of the promontorium of the pars petrosa. The foramen ovale is also situated far posteriorly at the posteroventral corner of the alisphenoid opposite the anterior part of the glenoid fossa; it is rimmed anteriorly by the alisphenoid and posteriorly by the anterior lamina of the petromastoid; its lateral margin touches the squamosal suture. The occipital plate slopes upwards and slightly forwards from the occipital condyles.

Nasal (Figs 11 and 12). — Anteriorly the nasals are elongate and subequal in breadth. At a point approximately dorsal to P2 they flare sharply laterally and posteriorly toward the frontal-maxilla suture, where their sutures with the frontals abruptly bend medially and, before meeting, make a sharp bend anteriorly. The nasal-frontal suture thus has a distinct W-shape, with the base of the W pointing posteriorly and the top anteriorly. The anterior-most edges of the nasals are broken in all specimens, but as suggested in YPFB Pal 6105 (right side) and 6110 in which they are most complete, they extended somewhat beyond their point of contact with the premaxilla and were apparently slightly longer medially.

Premaxilla (Fig. 12). — In dorsal and lateral views the premaxilla is sharply V-shaped. The ascending process is directed posteriorly between the nasal and maxilla and its posterior extremity

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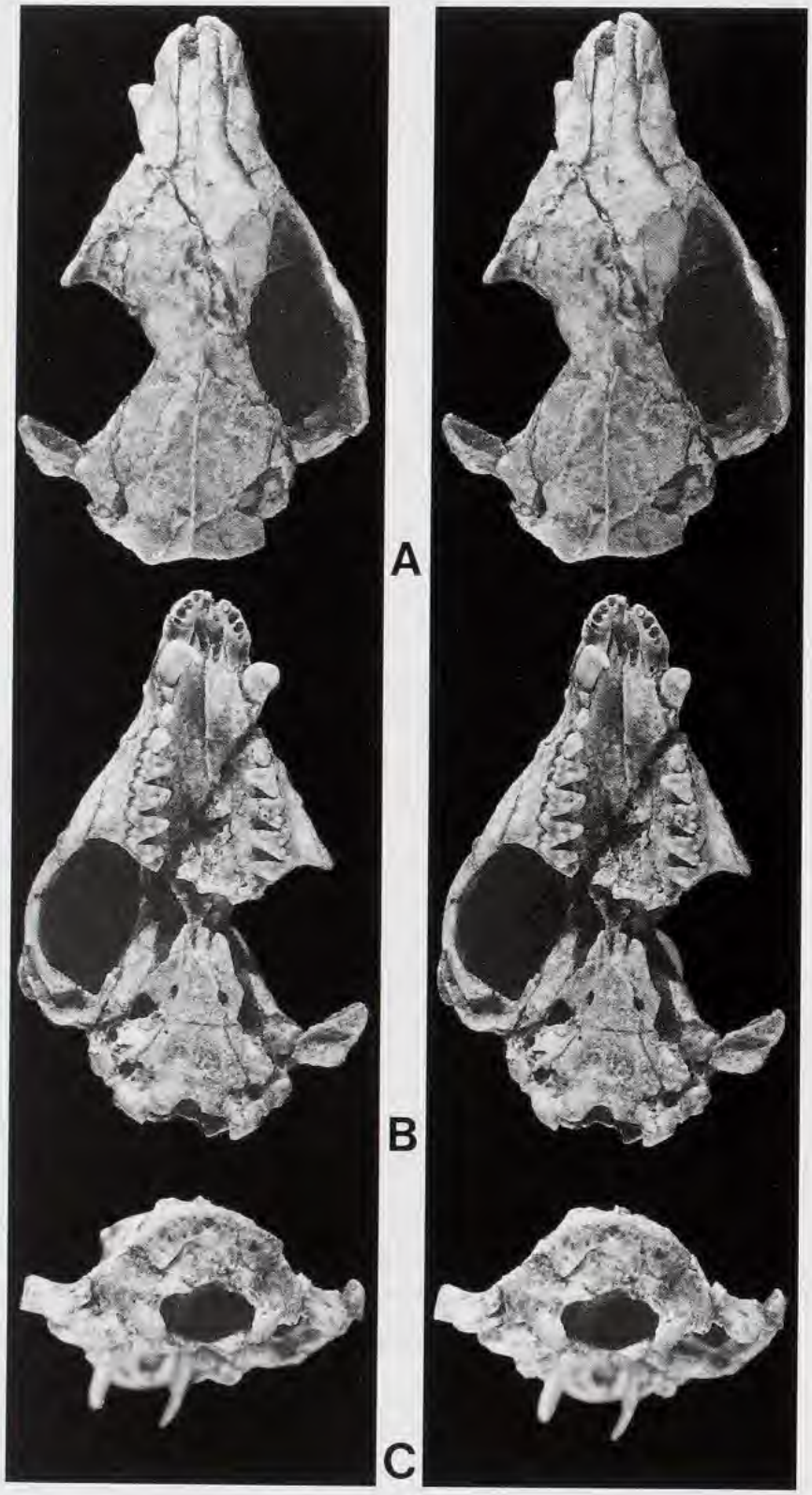

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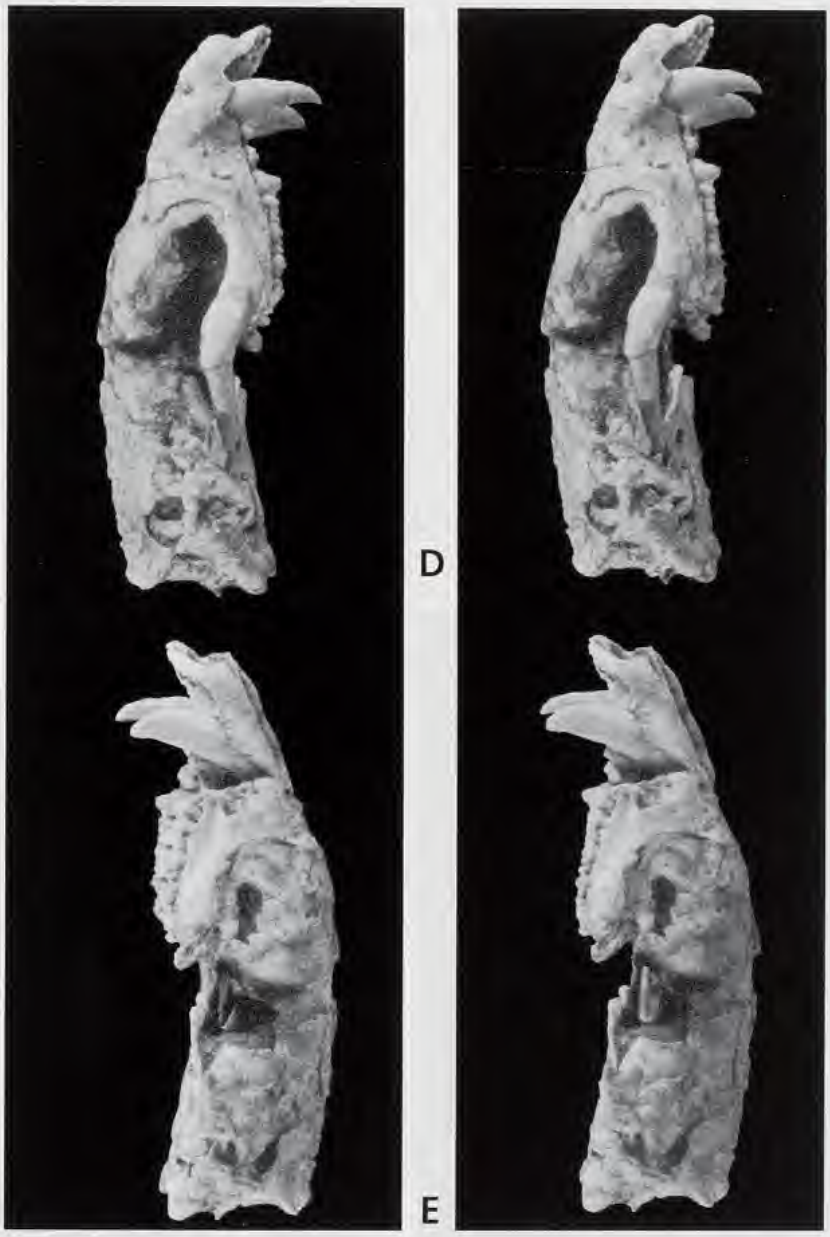

FIG. 10. —*Pucadelphys andinus*. Skull of YPFB Pal 6105 (holotype) (A, dorsal; B, ventral; C, occipital; D, right lateral; E, left lateral views). Stereophotos X 2.5.

FIG. 10. — Pucadelphys andinus. *Crâne d'YPFB Pal 6105 (holotype) (A, vue dorsale ; B, vue ventrale ; C, vue occipitale ; D, vue latérale droite ; E, vue latérale gauche). Photos stéréoscopiques X 2.5.*

Source : MNHN, Paris

is dorsal to the middle of C1. The ascending process of the premaxilla forms the dorsolateral edge of the nares and its lateral surface is slightly convex. The anterior edges of the two premaxillae have a distinctly rounded (sharply convex) shape when viewed dorsally. In ventral view the premaxilla-maxilla suture extends posteromedially from the anterior-most edge of the maxilla (lateral to I4), across the fossa which receives c1. Medially to the anterior mid-point of C1, the suture bends anteromedially and reaches the lateral edge of the incisive foramen in its posterior quarter. On the medial edge of the incisive foramen, the premaxilla-maxilla suture runs posteromedially from the posterior quarter of the foramen to the median plan of the skull. The paired incisive foramina are well developed and elongate anteroposteriorly, extending from a point medial to I3, anteriorly and to a point medial to the anterior edge of C1, posteriorly. The anterior 75% of the bar separating the incisive foramina medially is formed by the premaxilla; the posterior 25% is formed by the maxilla.

MAXILLA (Figs 12 and 15). — A small wing of the anterolateral edge of the maxilla overlaps the posterolateral edge of the premaxilla to a point labial to I5 and forms the lateral rim of the fossa between I5 and C1 (Fig. 12). Posterodorsally, the maxilla is wedged between the nasal and lacrimal, and has a small, but clear, contact with the frontal. From the posterior edge of the frontal-maxilla suture, the maxilla-lacrimal suture runs in an anterior direction, then anteroventrally along

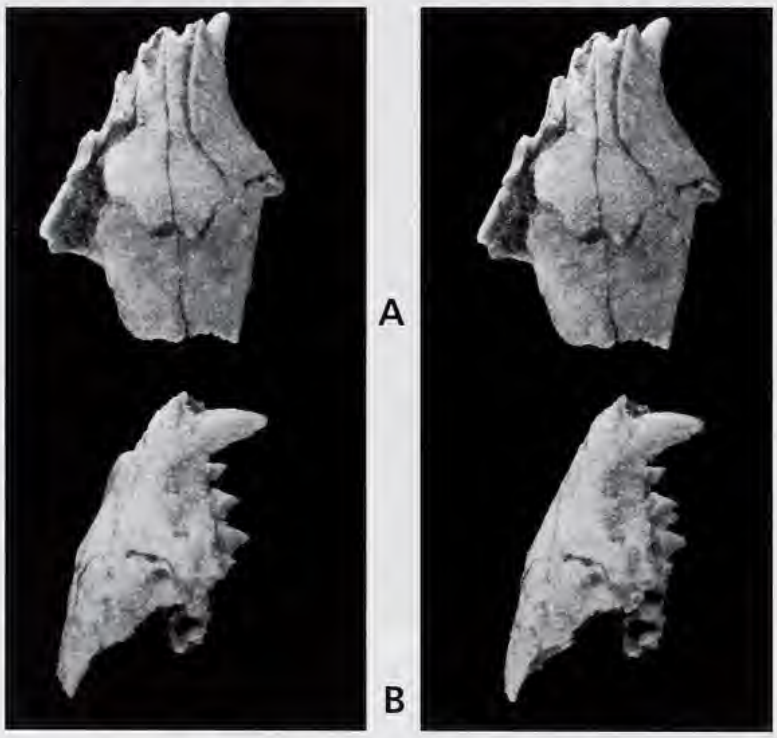

FIG. 11. —*Pucadelphys andinus*. Rostral part of skull of YPFB Pal 6109 (A, dorsal; B, right lateral views). Stereophotos X 2.5.

FIG. 11. — Pucadelphys andinus. *Portion rostrale du crâne d'YPFB Pal 6109 (A, vue dorsale; B, vue latérale droite). Photos stéréoscopiques X 2.5.*

Source : MNHN, Paris

the anterior rim of the orbit, contacting the jugal at the lower edge of the orbit dorsal to the posterior edge of M2. From that point, as seen in lateral and ventral views, the maxilla-jugal suture extends in a straight line posteroventrally.

The anterior (rostral) opening of the infraorbital canal is large, slightly elongate dorsoventrally (the ventral edge is slightly broader than the dorsal edge), and opens dorsal to P3. The posterior (orbital) opening is also large, slightly elongate transversely. The dorsal rim is formed by the lacrimal, the ventral and lateral rims by the maxilla, and the ventromedial rim by a sliver of the palatine which extends anteriorly between the lacrimal and maxilla into the infraorbital canal, as is clearly seen on left side of YPFB Pal 6105 (Fig. 15). The infraorbital canal transmits the infraorbital branch of V2, a branch of the infraorbital artery to the mesial side of maxilla and premaxilla, and a small vein in Recent metatherians (ARCHER, 1976a).

Within the orbit the maxilla forms the floor and, along its medial edge, has a broad contact with the palatine. The large postpalatine foramen is bordered by the maxilla laterally and by the palatine dorsally, medially and ventrally (Fig. 15).

In ventral view (Fig. 12), the posteromedial edge of the maxilla extends anteromedially from the lateral side of the postpalatine foramen, roughly parallel to the lingual edges of M3-4, and apparently has a broad transverse contact with the palatine medial to the embrasure between M2 and M3. This area of the palate is broken in all specimens and the suture itself is not visible; however, the relatively complete palate in YPFB Pal 6105 shows no vacuities in the palatal portion of the maxilla.

PALATINE (Figs 10 and 12). — The palatine contribution to the secondary palate is preserved only in YPFB Pal 6105 where it is nearly complete. The posterior edge of the palatine is a transversely thickened bar, the postpalatine torus, which extends below the level of the palate and which it encloses posteriorly. This torus lies posterior to the M4's and its maximum thickness is located laterally, posterior to the protocone's of the M4's. A large ovoid postpalatine foramen (which probably transmits the descending palatine vein, palatine artery and palatine branch of cranial nerve V) occurs at the posterolateral corner of the palatine (as seen only on the left side of YPFB Pal 6105). This foramen is clearly seen in anterior and posterior views, while in ventral view only the anteriormost edge is visible since the foramen is tucked above the postpalatine torus and opens vertically. The posterior surface of the postpalatine torus is ornamented by three spines: a lateral one on either side at the medial edge of the postpalatine foramen and a medial one at the contact of the two palatines. These spines give the ventral surface of the choanal orifice a broad m-shaped appearance. Immediately anterior to the torus and situated medially on each palatine is a pair of shallow parallel sulci (palatine sulci) which run anteriorly and probably extended to a middle palatine foramen as occurs in living *Didelphis*, although this foramen is not preserved in specimens of *Pucadelphys*. The anterior extent of the palatine is not fully preserved and the presence or absence of vacuities cannot be securely established, although if vacuities were present they were small. Given the relatively complete palate of YPFB Pal 6105, and the apparent absence of vacuities, the palate is shown as solid in the reconstruction (Fig. 12).

Part of the orbital or laterovertical process of the palatine is preserved in YPFB Pal 6105 (left side), 6108 (left side) and 6110 (right side) (Fig. 15). A large elliptical sphenopalatine foramen, which transmits the sphenopalatine artery and nerve into the naso-pharyngeal space above the

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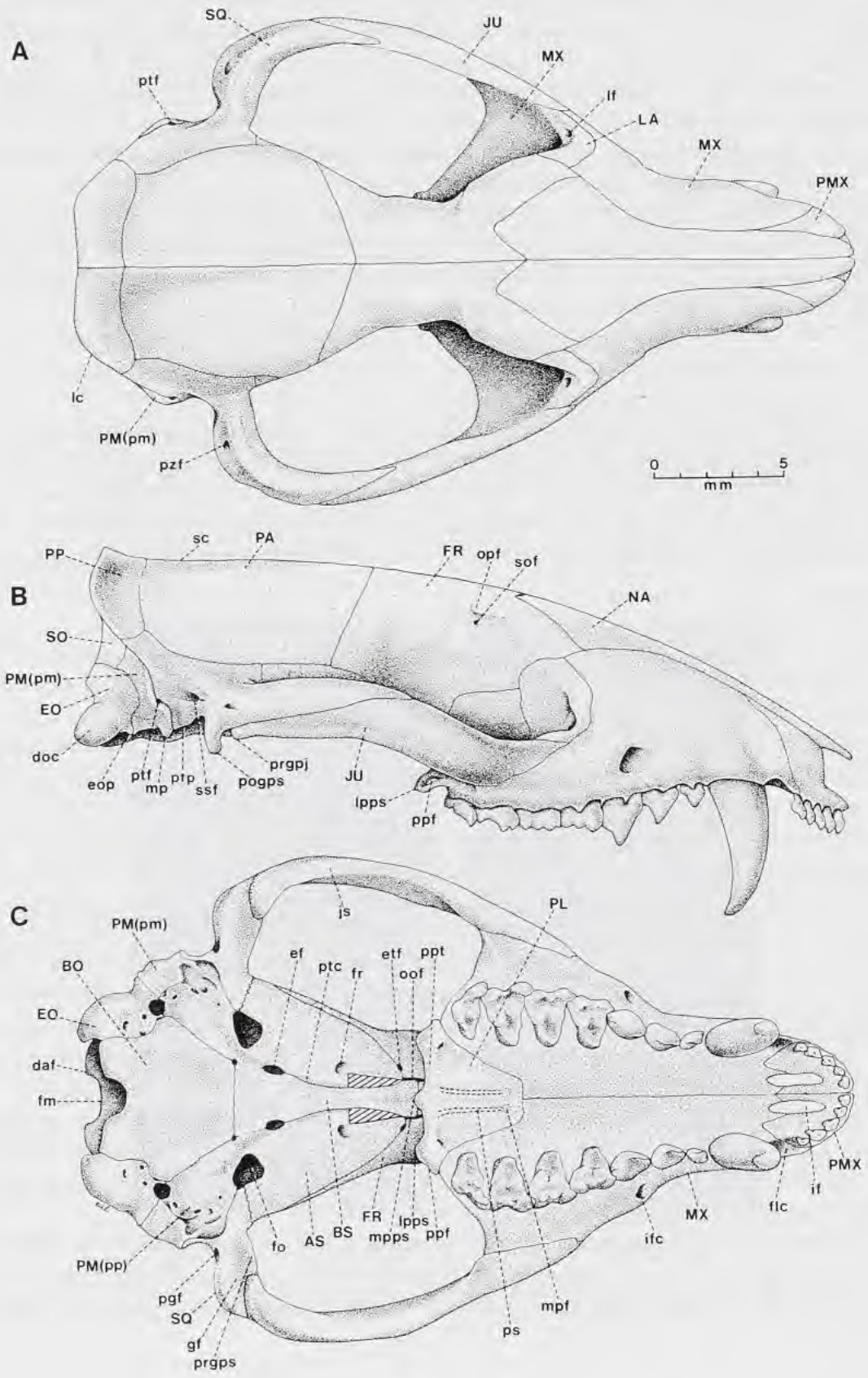

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palate, has a posteriorly directed opening within the vertical surface of the palatine at the posteromedial edge of the orbit just dorsomedial to the postpalatine foramen.

The palatine makes a small contribution to the medial edge of the orbital floor, extending medially in sutural contact with the maxilla from the lateral side of the postpalatine foramen, then almost directly anteriorly into the ventromedial corner of the infraorbital canal (Fig. 15). Its contact with the lacrimal is a broad suture extending ventrally from the anterior point of contact with the frontal to the lower edge of the infraorbital canal, where it turns sharply anterodorsally into that canal. Dorsally the palatine has a broad and nearly horizontal contact with the frontal; this suture extends posteriorly to a point above the sphenopalatine foramen where it bends ventroposteriorly to a point just posterodorsal to that foramen, then extends posteriorly along the ventrolateral edge of the orbitosphenoid, and has a small contact posteriorly with the anterior edge of the basisphenoid (as seen in YPFB Pal 6105, left side) (Fig. 15).

LACRIMAL (Figs 12 and 15). — This bone forms the anterior rim of the orbit. In dorsolateral view, the large facial wing of the lacrimal has a distinct quarter-moon shape. Viewed posterolaterally (Fig. 15), the lacrimal has a rectangular shape (long axis is dorsoventral) and contacts the maxilla anterodorsally, anteriorly and ventrolaterally, the jugal anteroventrally, the frontal dorsoposteriorly, and the palatine ventroposteriorly and ventromedially. The large elliptical shaped lacrimal

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FIG. 12. — *Pucadelphys andinus*. Reconstruction of the skull (A, dorsal; B, right lateral; C, ventral views) based primarily on YPFB Pal 6105 (holotype). Abbreviations: **AS**, alisphenoid; **BO**, basioccipital; **BS**, basisphenoid; **daf**, dorsal atlantal facet; **doc**, dorsal occipital condyle; **ef**, entocarotid foramen (=anterior carotid foramen, carotid canal); **EO**, exoccipital; **eop**, exoccipital process; **etf**, ethmoid foramen; **flc**, fossa for lower canine; **fm**, foramen magnum; **fo**, foramen ovale; **FR**, frontal; **fr**, foramen rotundum; **gf**, glenoid fossa; **if**, incisive foramen; **ifc**, infraorbital canal; **JU**, jugal; **js**, jugular sulcus; **LA**, lacrimal; **lc**, lambdoidal crest (=nuchal crest); **lf**, lacrimal foramen; **lpps**, lateral postpalatine spine; **mp**, mastoid process; **mpf**, middle palatine foramen; **mpps**, medial postpalatine spine; **MX**, maxilla; **NA**, nasal; **oof**, optic-orbital foramen; **opf**, supraorbital process of frontal; **PA**, parietal; **pgf**, postglenoid foramen; **PL**, palatine; **PM(pm)**, pars mastoidea of petromastoid (=mastoid s.s.); **PM(pp)**, pars petrosa of petromastoid (=petrosal s.s.); **PMX**, premaxilla; **pogps**, postglenoid process of squamosal; **PP**, postparietal; **ppf**, postpalatine foramen; **ppt**, postpalatine torus; **prgpj** preglenoid process of jugal; **prgps**, preglenoid process of squamosal; **ps**, palatine sulcus; **ptc**, pterygoid canal; **ptf**, posttemporal foramen; **ptp**, posttympanic process; **pzf**, postzygomatic foramen; **sc**, sagittal crest; **SO**, supraoccipital; **sof**, supraorbital foramen; **SQ**, squamosal; **ssf**, subsquamosal foramen (=suprameatal, postsquamosal).

FIG. 12. — Pucadelphys andinus. *Reconstitution du crâne (A, vue dorsale; B, vue latérale droite; C, vue ventrale) principalement d'après YPFB Pal 6105 (holotype). Abréviations:* ***AS****, alisphénoïde;* ***BO****, basioccipital;* ***BS****, basisphénoïde;* ***daf****, facette atlantale dorsale;* ***doc****, condyle occipital dorsal;* ***ef****, foramen entocarotidien (=foramen carotidien antérieur, canal carotidien);* ***EO****, exoccipital;* ***eop****, processus exoccipital ;* ***etf****, foramen ethmoïdien;* ***flc****, fosse pour la canine inférieure;* ***fm****, foramen magnum;* ***fo****, foramen ovale;* ***FR****, frontal;* ***fr****, foramen rotundum;* ***gf****, fosse glénoïde;* ***if****, foramen incisif;* ***ifc****, canal infraorbitaire;* ***JU****, jugal;* ***js****, sillon jugulaire;* ***LA****, lacrimal;* ***lc****, crête lambdoïde (=crête nuchale);* ***lf****, foramen lacrimal;* ***lpps****, épine postpalatine latérale;* ***mp****, processus mastoïde;* ***mpf****, foramen palatin moyen;* ***mpps****, épine postpalatine médiale;* ***MX****, maxillaire;* ***NA****, nasal;* ***oof****, foramen optico-orbitaire;* ***opf****, processus supra-orbitaire du frontal;* ***PA****, pariétal;* ***pgf****, foramen postglénoïde ;* ***PL****, palatin;* ***PM(pm)****, pars mastoidea du pétreux (=mastoïde s.s.);* ***PM(pp)****, pars petrosa du pétromastoïde (=pétreux s.s.);* ***PMX****, prémaxillaire;* ***pogps****, processus postglénoïde du squamosal;* ***PP****, postpariétal;* ***ppf****, foramen postpalatin;* ***ppt****, torus postpalatin;* ***prgpj*** *processus préglénoïde du jugal;* ***prgps****, processus préglénoïde du squamosal;* ***ps****, sillon palatin;* ***ptc****, canal ptérygoïde;* ***ptf****, foramen posttemporal;* ***ptp****, processus posttympanique;* ***pzf****, foramen postzygomatique;* ***sc****, crête sagittale;* ***SO****, supraoccipital;* ***sof****, foramen supraorbitaire;* ***SQ****, squamosal;* ***ssf****, foramen subsquamosal (=supraméatal, postsquamosal).*

Source : MNHN, Paris

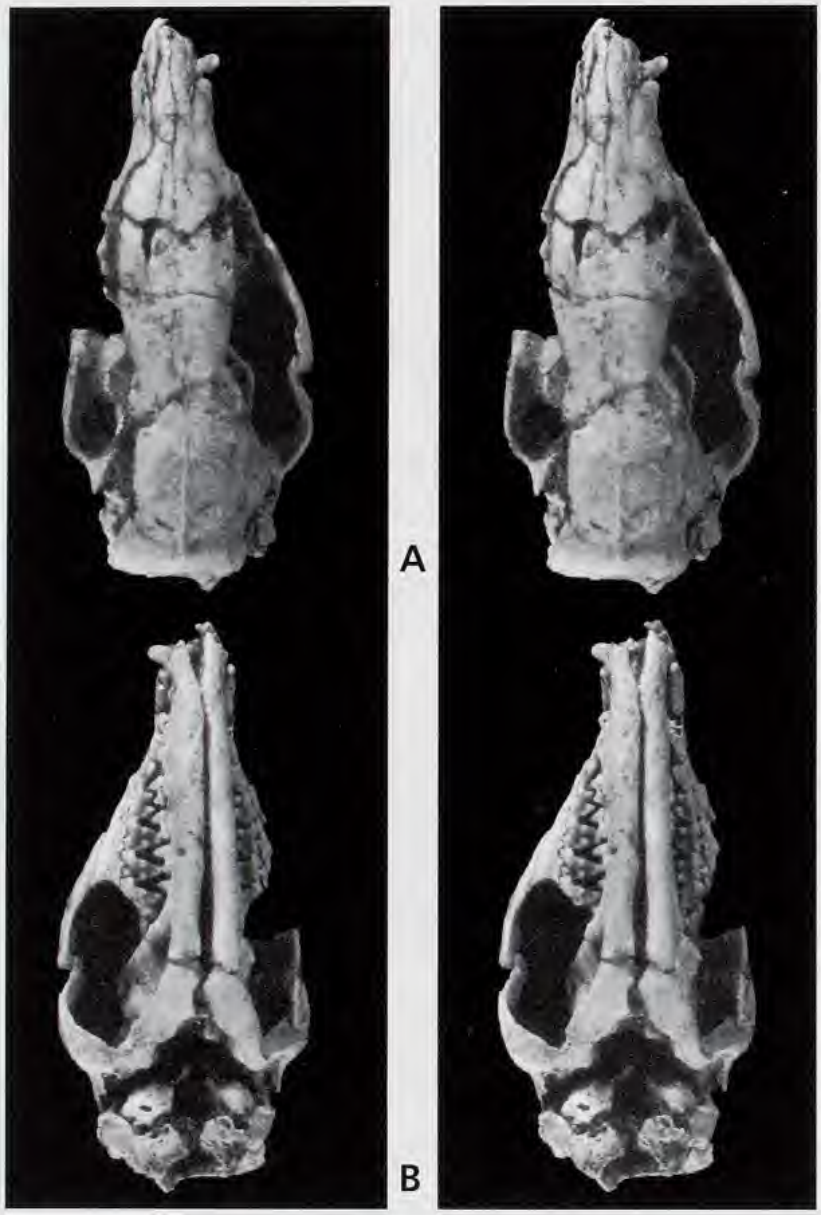


FIG. 13. — *Pucadelphys andinus*. A-C, skull with attached mandible of YPFB Pal 6110 (A, dorsal; B, ventral; C, right lateral views). Stereophotos X 2.5.

FIG. 13. — Pucadelphys andinus. *A-C, crâne et mandibule en connexion d'YPPFB Pal 6110 (A, vue dorsale; B, vue ventrale; C, vue latérale droite). Photos stéréoscopiques X 2.5.*

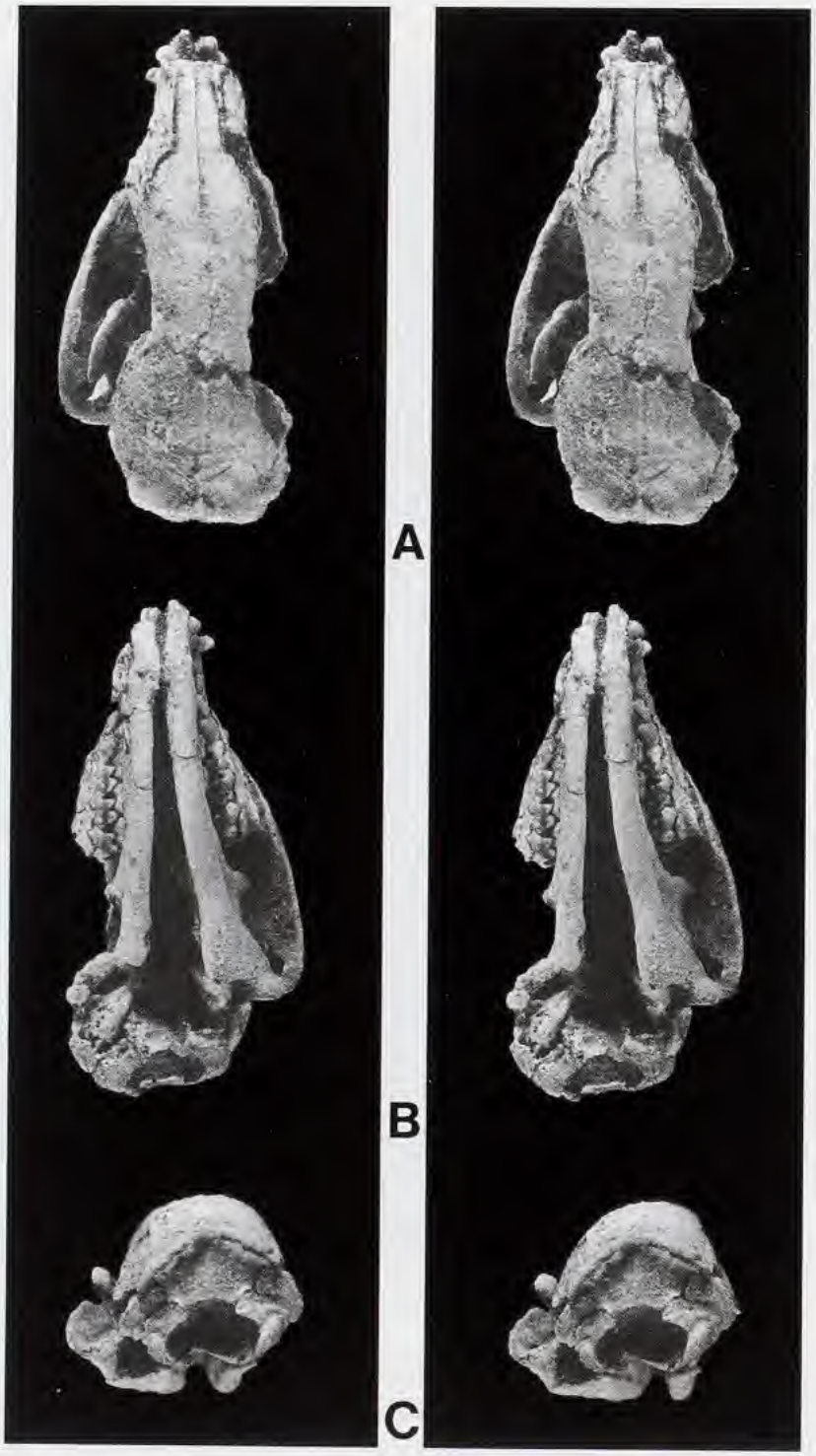
Source : MNHN, Paris

foramen, which transmits the naso-lacrimal duct, opens within the orbit and has two distinct canals of subequal size situated one above the other along a dorsomedial-ventrolateral axis (Fig. 15).

JUGAL (Fig. 12). — Complete jugals are preserved in YPFB Pal 6105 (right side) and 6471 (left side). This is a large bone which contributes to the formation of about 60% of the zygomatic arch. Anteriorly it has a broad diagonal contact with the maxilla, a small contact with the lacrimal anterodorsally-anteromedially, and it forms the ventral edge of the orbital rim. From its contact with the maxilla it arcs in a posterolaterodorsal direction, being dorsoventrally deep and transversely narrow. At its dorsal and lateral greatest extent, which is approximately lateral to the interorbital constriction, the jugal makes contact with the zygomatic process of the squamosal dorsally and continues ventrally along it to the anterolateral edge of the glenoid fossa where it forms a large preglenoid process. In lateral view, the ventroposterior spine of the jugal and dorsal zygomatic process of the squamosal have an elongate diagonal contact (Fig. 12). A shallow sulcus occurs along the ventrolateral edge of the jugal contribution to the zygomatic arch marking the point of insertion of the masseter muscle (Fig. 12). The greater part of the zygomatic arch, including the jugal and squamosal contributions, is subequal in breadth and depth.

FRONTAL (Figs 12 and 15). — This bone covers all of the medial 30% of the dorsal area and most of the medial 30% of the lateral area of the cranium. Anteriorly it has a distinct W-shaped contact with the nasals (Fig. 12), and lateral to this is a small distinct contact with the maxilla. The lacrimal contact is broad and nearly horizontal dorsally, and broad but nearly vertical laterally. There is a broad nearly horizontal contact with the dorsal edge of the orbital part of the palatine, and a small wedge of the frontal extends ventrally and separates the palatine and orbitosphenoid

Source : MNHN, Paris



Source : MNHN, Paris

FIG. 14. — *Pucadelphys andinus*. Skull with attached mandible of YPFB Pal 6107 (A, dorsal; B, ventral; C, posterior; D, left lateral views). Stereophotos X 2.5.

FIG. 14. — Pucadelphys andinus. *Crâne et mandibule en connexion d'YPFB Pal 6107 (A, vue dorsale; B, vue ventrale; C, vue postérieure; D, vue latérale gauche). Photos stéréoscopiques X 2.5.*

(Fig. 15). The frontal contacts the small orbital contribution of the orbitosphenoid along its anterior and dorsal edges. More posteriorly, the frontal has a broad arcuate contact with the alisphenoid, ventral to the interorbital constriction on the anterior surface of the cranium. The contact with the parietal extends from the lateral surface of the anterior part of the cranium in an almost straight line dorso-dorsoanteriorly, just posterior to the interorbital constriction. A weak supraorbital process is sometimes present (as in YPFB Pal 6105 and 6108) on the anterolateral surface of the frontal, and a small anteriorly opening supraorbital foramen consistently occurs just ventral to this process within the dorsal edge of the orbit. A well developed oval-shaped ethmoid foramen opens anteriorly at the frontal-alisphenoid-orbitosphenoid contact. The anteromedial and dorsal wall of this foramen are formed by the frontal, the posterolateral wall by the alisphenoid, the anteroventral wall by the orbitosphenoid, and the posteroventral wall by the basisphenoid as seen in YPFB Pal 6105 (right side) and 6108 (left side).

PARIETAL (Fig. 12). — The large plate-like parietals cover the greater part of the dorsal and dorsolateral surfaces of the cranium. They have a broad ventroposteriorly directed contact with the frontal, a broad continuous contact with the dorsal parts of the alisphenoid and squamosal ventrally, and a broad convex contact with the postparietal posteriorly. The outer walls of the parietals are distinctly convex, reflecting the presence of well developed cerebral hemispheres, and are ornamented dorsomedially by irregular scars for attachment of the temporalis muscle.

Source : MNHN, Paris

These scars are seen to some degree in all specimens, but are most prominent in YPFB Pal 6105 in which a distinct scar-region on the left parietal extends from the frontal-parietal suture directed toward, but not reaching, the postparietal-squamosal suture. On the right parietal of YPFB Pal 6105 and in all other specimens these scars are less distinct and are concentrated on the dorsomedial area of this bone.

POSTPARIETAL (Figs 12 and 17). — This bone is tightly fused with the parietal and the suture is often difficult to identify. Nevertheless, careful study shows that the contact with the parietal is broadly concave and extends ventrally where it meets the dorsoposterior end of the squamosal, then turns sharply posteriorly having a nearly horizontal suture with the squamosal. A distinct suture separates the postparietal from the underlying supraoccipital (Fig. 17). The postparietal overhangs the entire dorsal edge of the supraoccipital so that the lambdoidal crest is formed entirely by the posterior edge of the postparietal. Viewed posteriorly the postparietal also overlaps the dorsolateral edge of the pars mastoidea of the petromastoids (Fig. 17).

ORBITOSPHENOID (Fig. 15). — Parts of this bone are preserved only in YPFB Pal 6105 and 6108. Viewed laterally this bone makes a small contribution to the posteroventral base of the orbital region. It contacts the frontal anteriorly and dorsally, the palatine anteroventrally and the basisphenoid posteroventrally. In ventral view it forms the posteromedial roof of the choanal orifice, the posterolateral parts of the roof are formed by small wings of the palatine. Within the orbit (Fig. 15) a large ovoid, anteriorly opening optic-orbital foramen (which transmits cranial nerves II, III, IV, V1, VI, the ophthalmic artery, and a vein which drains the eye to the cavernous sinus) has the entire medial wall formed by the orbitosphenoid, the anteroventral edges by the palatine, the anterior and dorsal edges by the frontal, and apparently the alisphenoid posterolaterally although the alisphenoid is broken in this area in all specimens. The posterior side of the orbitosphenoid has a distinct convex saddle-shaped surface marking the confluence of the left and right optic-orbital foramina; the posterodorsal part has the form of laterally projecting horns which separate the upper edge of the optic-orbital foramen from the lower edge of the more dorsally situated ethmoid foramen.

ALISPHENOID (Figs 12, 15, and 19). — This bone forms most of the anterior ventrolateral parts of the ventral surface of the cranium. Anterodorsally it has a broad horizontal contact with the frontal (Fig. 15); posterodorsally a broad horizontal contact with the parietal; posteriorly a broad convex contact with the squamosal, which continues ventrally toward the base of the zygomatic process, passes anteriorly around it, continues on the ventral surface of the skull and reaches the posterolateral corner of the foramen ovale (which transmits V3, and possibly the major transverse sinus of the external jugular vein; see below) (Figs 12 and 19). The alisphenoid forms the anterior rim of the foramen ovale and, at its contact with the petromastoid, lateral to the position of the small medial lacerate foramen (which is located at the junction of the basisphenoid-basioccipital-petromastoid-alisphenoid; *sensu* MACINTYRE, 1967) it extends anteriorly in tight sutural contact with the basisphenoid, bisects the entocarotid foramen (alisphenoid forms lateral rim, basisphenoid

Source : MNHN, Paris

medial rim), which transmits the internal carotid artery and a small vein from the inferior petrosal sinus, and continues anteriorly to the anterior edge of the basisphenoid. The anteroventral extent of the alisphenoid is not preserved in any specimen, but it probably formed the posterolateral rim of the optic-orbital foramen as in *Didelphis*, and based on the size and breakage surface anteroventrally there was clearly a wing-like structure which extended anterolaterally toward the lateral edge of the choanal orifice (Fig. 15). On the anteroventral surface, immediately lateral and parallel to the basisphenoid contact, is a sulcus marking the position of the pterygoid canal (for the pterygoid or vidian nerve; see JOLLIE, 1962: 44) or sutural contact with the pterygoid (seen in YPFB Pal 6105). This bone is not well preserved in any specimen. The pterygoid canal can be followed posteriorly to the anterolateral edge of the entocarotid foramen. Immediately lateral and slightly dorsal to this canal is a large ovoid, anteriorly opening foramen rotundum (seen only in YPFB Pal 6108) which transmitted the maxillary branch of the trigeminal nerve, V2 (JOLLIE, 1962: 44) (Figs 12 and 15).

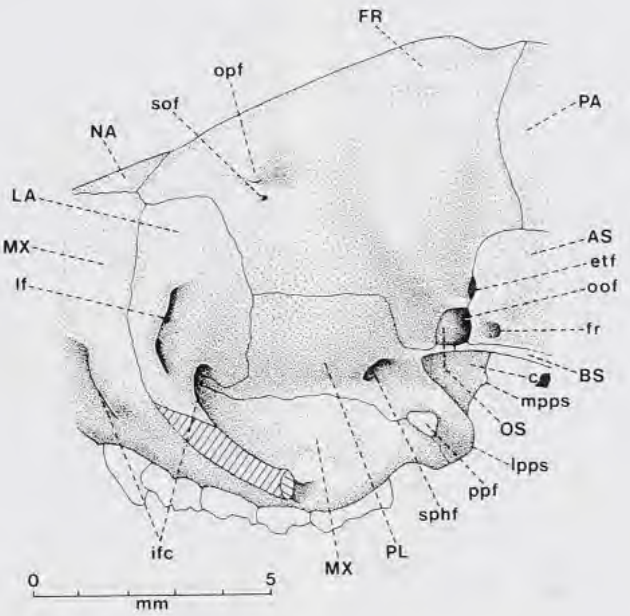


FIG. 15. — *Pucadelphys andinus*. Detail of left orbital region based primarily on YPFB Pal 6105 (holotype). Abbreviations: **AS**, alisphenoid; **BS**, basisphenoid; **co**, choanal orifice; **etf**, ethmoid foramen; **fr**, foramen rotundum; **FR**, frontal; **ifc**, infraorbital canal; **LA**, lacrimal; **lf**, lacrimal foramen; **mpps**, medial postpalatine spine; **MX**, maxilla; **NA**, nasal; **oof**, optic-orbital foramen; **opf**, supraorbital process of frontal; **OS**, orbitosphenoid; **PA**, parietal; **PL**, palatine; **ppf**, postpalatine foramen; **sof**, supraorbital foramen; **sphf**, sphenopalatine foramen.

FIG. 15. — Pucadelphys andinus. *Détail de la région orbitaire gauche principalement d'après YPFB Pal 6105 (holotype). Abréviations: **AS**, alisphénoïde; **BS**, basisphénoïde; **co**, orifice de la choane; **etf**, foramen ethmoïde; **fr**, foramen rotundum; **FR**, frontal; **ifc**, canal infraorbitaire; **LA**, lacrimal; **lf**, foramen lacrimal; **mpps**, épine postpalatine médiale; **MX**, maxillaire; **NA**, nasal; **oof**, foramen optico-orbitaire; **opf**, processus supraorbitaire du frontal; **OS**, orbitosphénoïde; **PA**, pariétal; **PL**, palatin; **ppf**, foramen postpalatin; **sof**, foramen supraorbitaire; **sphf**, foramen sphénopalatin.*

Source : MNHN, Paris

BASISPHENOID (Figs 12 and 15). — As seen in YPFB Pal 6105 and 6108, this is an anteroposteriorly elongate bone which is broadest posteriorly along its contact with the basioccipital and narrows anteriorly to its contact with the orbitosphenoid; sutures with the basioccipital and orbitosphenoid are distinct. Laterally it has broad contacts with the alisphenoid; these bones are tightly fused and the suture is, in places, difficult to identify. The posterior surface of the basisphenoid is convex ventrally, while anterior to the entocarotid foramen it is flat. The anterior end of this bone in YPFB Pal 6105 is broken transversely, a feature which appears to represent natural breakage but which may mark sutural contact between the basisphenoid (s.s.) and a smaller presphenoid. However, this bone is quite similar to that in *Didelphis* and appears to be the basisphenoid which is simply lacking its anterior end.

SQUAMOSAL (Figs 12, 17 and 19). — This bone has a broad concave contact with the alisphenoid anteriorly; a broad and nearly horizontal contact with the parietal dorsoanteriorly and dorsomedially, and with the postparietal dorsoposteriorly; an irregular vertical contact with the lateral surface of the pars mastoidea of the petromastoid posteriorly; and ventrally its contact with the petromastoid extends anteromedially from the lateral base of the mastoid process, passes along the lateral edge of the fossa incudis and epitympanic recess, and joins the short transversely oriented squamosal suture at the posterolateral corner of the foramen ovale.

In ventral view the glenoid fossa is deep and transversely elongate; a large postglenoid process of the squamosal occurs along its posterior edge and attains its greatest ventral extension medially; a much lower, but still distinct, preglenoid process of the squamosal occurs along the anteromedial edge of the fossa and a large preglenoid process of the posterior edge of the jugal borders the fossa anterolaterally.

Three foramina perforate the squamosal externally. The first and smallest is a postzygomatic foramen on the posterobasal surface of the zygomatic arch dorsal to the deepest point of the postglenoid process (Fig. 17). This foramen apparently transmits a vein from the squamosal root of the zygomatic arch to the sphenoparietal emissary vein (ARCHER, 1976a). It is usually single, transversely elongate, and opens laterally; however, it is sometimes double (as in left side of YPFB Pal 6105) with a second smaller opening set dorsomedially to the primary one.

The second foramen is the subsquamosal which is large, oval, and opens posteroventrally at the base of the zygomatic arch just dorsal to the external acoustic meatus (Fig. 12). It is most clearly seen in posterolateral view, while in dorsal view it is obscured by a posterior swelling of the squamosal along its upper edge and a similar but smaller swelling occurs along its lower edge. Thus, this foramen opens into a shallow postzygomatic depression in the squamosal. Externally the foramen opens within the squamosal, while internally (as seen in right side of YPFB Pal 6110) the medial side of the canal that it transmits is formed by the petromastoid and the lateral side by the squamosal (Fig. 19). This foramen transmits an artery from the postglenoid foramen onto the parietal area of the cranium which supplies the temporalis muscle, and a vein from the parietal area to the sphenoparietal emissary vein, which exits through the postglenoid foramen (ARCHER, 1976a; WIBLE, 1990).

Source : MNHN, Paris

The third and largest is the postglenoid foramen which is ovoid in shape and opens ventrolaterally along the posteromedial edge of the postglenoid process (Figs 12 and19). The course of the vessels this foramen transmits continues as a groove beyond the opening toward the ventromedial edge of the postglenoid process. The external opening occurs solely within the squamosal, while internally (as seen on the right side of YPFB Pal 6110; Fig. 19) at a level corresponding to the dorsal rim of the external acoustic meatus, the medial side of this canal is formed by the petromastoid and the lateral side by the squamosal. This foramen transmits the

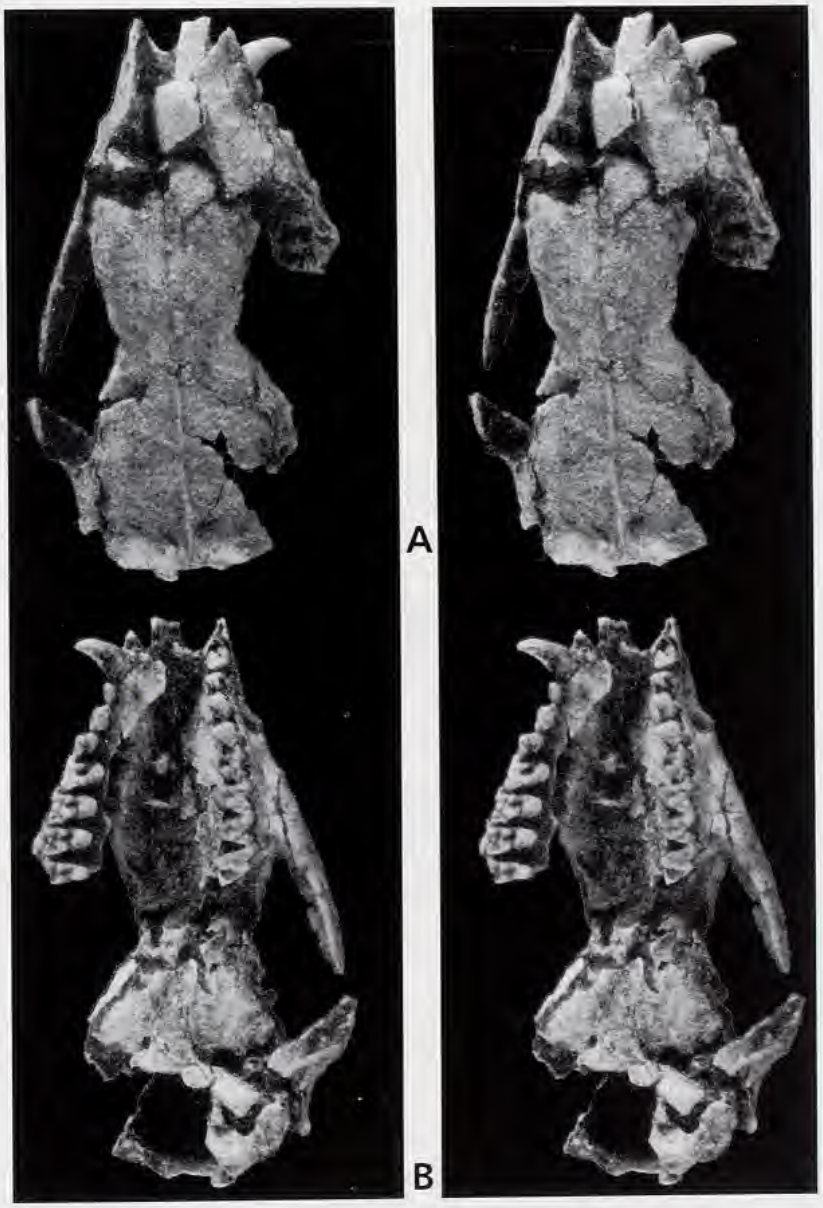


FIG. 16. — *Pucadelphys andinus*. Skull of YPFB Pal 6108 (A, dorsal; B, ventral views). Stereophotos. X 2.5.

FIG. 16. — Pucadelphys andinus. *Crâne d'YPFB Pal 6108 (A, vue dorsale; B, vue ventrale). Photos stéréoscopiques. X 2.5.*

Source : MNHN, Paris

sphenoparietal emissary (which externally becomes the postglenoid) vein from the prootic sinus (WIBLE, 1990), and the postglenoid artery (ARCHER, 1976a; WIBLE, 1990).

A fourth but smaller foramen, the posttemporal, opens between the squamosal and pars mastoidea of the petromastoid directly posterior to the subsquamosal foramen and dorsal to the mastoid process. This foramen transmits the arteria diploetica magna and vena diploetica magna (WIBLE, 1990) which pass through a canal bordered by the petromastoid medially and squamosal laterally (Fig. 21).

BASIOCCIPITAL (Figs 12, 17, 19 and 21). — As seen in YPFB Pal 6105, 6107 and 6470, this bone has the shape of an arrow-head base and the sutures with adjacent elements are well defined. The basioccipital has a broad transverse linear contact with the basisphenoid anteriorly between the left and right medial lacerate foramina. From these foramina it extends posterolaterally in contact with the medial surface of the pars petrosa of the petromastoid to the anteromedial corner of the posterior lacerate foramen, where it bends sharply medially forming a small but distinct convex rim over the inferior petrosal foramen (basioccipital forms ventral and medial rims, exoccipital forms ventromedial rim, and pars petrosa of petromastoid forms lateral rim) which transmits the inferior petrosal sinus. On the medial side of the foramen for the inferior petrosal sinus the basioccipital contacts the exoccipital and the suture arcs posteromedially to a point on the lateral side of the ventral occipital condyle. The posterior edge of the basioccipital forms the ventral rim of the foramen magnum where a pair of well developed ventral occipital condyles are separated by a distinct U-shaped intercondylar fossa. The foramen magnum transmits most of the sigmoid sinus of the transverse venous system and the spinal root of nerve XI out of cranium (DOM *et al.*, 1970; WIBLE, 1990) and the vertebral arteries into cranium (ARCHER, 1976a).

The ventral surface of the basioccipital has a low medial keel extending anteriorly from the middle of the intercondylar fossa to the basisphenoid suture; the lateral edges of the basioccipital are elevated surfaces extending parallel to the petromastoid suture and they mark the floor of the inferior petrosal sinus; between each of these lateral elevations and the medial keel is a broad fossa for the rectus capitis muscle; the posterolateral edge of the basioccipital, between the elevated ventral occipital condyles and the ventral rim of the inferior petrosal foramen, is distinctly convex dorsally.

EXOCCIPITAL (Figs 12, 17, 19 and 21). — Viewed ventrally this bone contacts the basioccipital medially; it forms the posterodorsal rim of the inferior petrosal foramen anteromedially; and the medial and posterior rim of the posterior lacerate foramen (which transmits nerves IX, X, XI and probably a small branch of the sigmoid sinus to the internal jugular vein) anteriorly; it also makes a small contact with the pars petrosa of the petromastoid via a septum between the inferior petrosal and posterior lacerate foramina; and laterally it contacts the pars mastoidea of the petromastoid.

Ventrally, in the large fossa just anterior to the elevated prominence of the lower rim of the dorsal occipital condyle, are typically three small subequal-sized condyloid foramina (Fig. 19) which apparently transmit branches of cranial nerve XII as occurs in some specimens of *Didelphis*

Source : MNHN, Paris

(JOLLIE, 1962: 55) but may also transmit branches of the sigmoid sinus to the internal jugular vein (ARCHER, 1976a, fig. 2B). Of these three foramina the posterior-most passes under the medial part of the dorsal occipital condyle; a second occurs anterolaterally between the first and posterior lacerate foramen; and the third occurs anterior to the first and opens either totally within the exoccipital just lateral to the basioccipital suture or within the suture itself.

Viewed posteriorly (Fig. 17) the exoccipital has a broad arcuate (convex) contact with the pars mastoidea of the petromastoid which extends from the center of the exoccipital process ventrally to the junction with the supraoccipital dorsally, where it bends sharply medially having a slight arcuate (convex) contact with the supraoccipital to the dorsal edge of the dorsal atlantal facet; medially, it forms the lateral rim of the posteriorly facing and transversely ovoid foramen magnum. On its posterior dorsomedial surface, the exoccipital has a prominent dorsal atlantal facet at the point of contact with the supraoccipital and a large ovoid dorsal occipital condyle occurs ventromedially. The exoccipital contributes to the formation of the medial half of the very small exoccipital process ventrolaterally. The exoccipital process is delimited medially by a trough in the exoccipital separating it from the dorsal occipital condyle, and another trough laterally in the petromastoid separating it from the larger mastoid process.

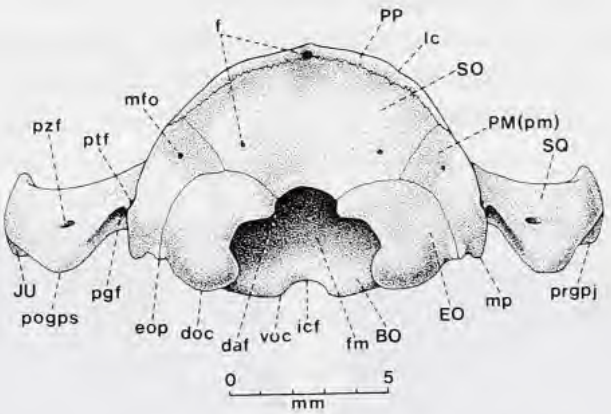


FIG. 17. — *Pucadelphys andinus*. Reconstruction of the posterior view of the skull and zygomatic arches, based primarily on YPFB Pal 6105 (holotype). Abbreviations: **BO**, basioccipital; **daf**, dorsal atlantal facet; **doc**, dorsal occipital condyle; **EO**, exoccipital; **eop**, exoccipital process; **f**, foramen; **fm**, foramen magnum; **icf**, intercondylar fossa; **JU**, jugal; **lc**, lambdoidal crest (=nuchal crest); **mfo**, mastoid foramen; **mp**, mastoid process; **pgf**, postglenoid foramen; **PM(pm)**, pars mastoidea of petromastoid (=mastoid s.s.); **pogps**, postglenoid process of squamosal; **PP**, postparietal; **prgpj** preglenoid process of jugal; **ptf**, posttemporal foramen; **pzf**, postzygomatic foramen; **SO**, supraoccipital; **SQ**, squamosal; **voc**, ventral occipital condyle.

FIG. 17. — Pucadelphys andinus. *Reconstitution de la vue postérieure du crâne et des arcades zygomatiques principalement d'après YPFB Pal 6105 (holotype). Abréviations:* ***BO****, basioccipital;* ***daf****, facette atlantale dorsale;* ***doc****, condyle occipital dorsal;* ***EO****, exoccipital;* ***eop****, processus exoccipital;* ***f****, foramen;* ***fm****, foramen magnum;* ***icf****, fosse intercondylienne;* ***JU****, jugal;* ***lc****, crête lambdoïde (=crête nuchale);* ***mfo****, foramen mastoïde;* ***mp****, processus mastoïde;* ***pgf****, processus postglénoïde;* ***PM(pm)****, pars mastoidea du pétromastoïde (=mastoïde s.s.);* ***pogps****, processus postglénoïde du squamosal;* ***PP****, postpariétal;* ***prgpj*** *processus préglénoïde du jugal;* ***ptf****, foramen posttemporal;* ***pzf****, foramen postzygomatique;* ***SO****, supraoccipital;* ***SQ****, squamosal;* ***voc****, condyle occipital ventral.*

Source : MNHN, Paris

In YPFB Pal 6105 the distance between the outer edges of the dorsal occipital condyles is 8.0 mm and 4.5 mm between the inner edges; the maximum breadth of the foramen magnum, dorsal to the dorsal occipital condyles, is 5.0 mm and the maximum depth is 3.0 mm.

SUPRAOCCIPITAL (Figs 12 and 17). — This bone occupies most of the dorsal surface of the occipital plate and forms the dorsomedial rim of the foramen magnum. It has a broad contact with the exoccipital ventrolaterally, a broad contact with the pars mastoidea of the petromastoid laterally, and a broad arcuate contact with the postparietal dorsally. As noted above, the contact with the latter occurs ventral to the lambdoidal crest which is formed entirely by the postparietal. The occipital area is hidden in dorsal view by the postparietal extension of the lambdoidal crest. There is no distinct vertical medial crest, but in YPFB Pal 6105 the posterior surface is ornamented with small ridges, scars and shallow pits marking areas of insertion of the nuchal muscle (these features are not seen in other specimens). There are only three small foramina in the supraoccipital: one (left and right) dorsomedial to the point of contact of the petromastoid and exoccipital; and a single foramen dorsomedially, between the supraoccipital and postparietal below the lambdoidal crest at its point of contact with the sagittal crest.

PETROMASTOID (Figs 12, 17, 19 and 21). — This is the most complex bone of the skull. For purposes of description it can be divided into two principal components: the pars mastoidea which contributes to the formation of the lateral part of the occipital region and houses the subarcuate fossa on the cerebellar side; and the pars petrosa which houses the inner ear in a teardrop shaped promontorium on the ventral side between the basioccipital and squamosal, and the internal acoustic meatus on the cerebellar side (MACINTYRE, 1972).

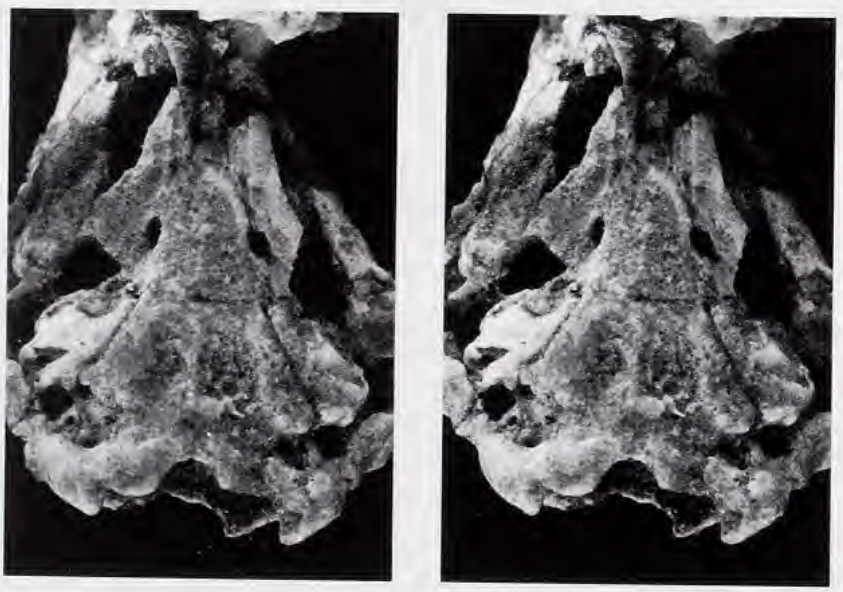


FIG. 18. — *Pucadelphys andinus*. Ventral view of basicranium of YPFB 6105 (holotype). Stereophotos, X 5.

FIG. 18. — Pucadelphys andinus. *Vue ventrale de la base du crâne d'YPFB 6105 (holotype). Photos stéréoscopiques, X 5.*

Source : MNHN, Paris

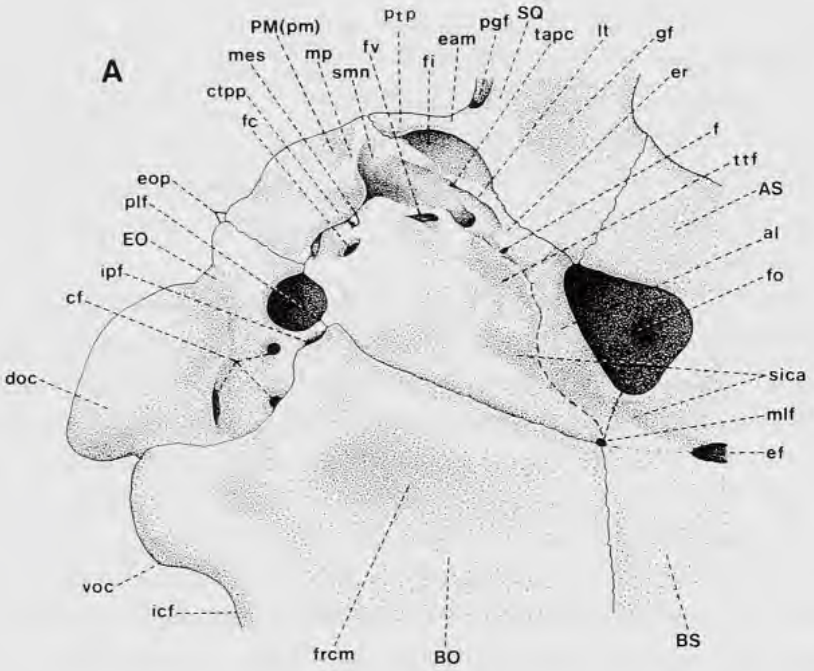
The pars mastoidea is best seen in posterior view (Fig. 19) where it occupies the lateral area of the occipital region and contacts the exoccipital ventromedially, the supraoccipital dorsomedially, the ventrolateral edge of the postparietal dorsally, and the squamosal along most of its lateral surface. A tiny mastoid foramen typically occurs on the posterior surface of the pars mastoidea just lateral to the supraoccipital-exoccipital-petromastoid juncture (Fig. 17), and internally opens along the posterior side of the sigmoid sinus (Fig. 21). A small posttemporal foramen (*sensu* WIBLE, 1990) occurs on the lateral surface of the occiput between the squamosal and the pars mastoidea (Figs 12 and 21; see below). A large ovoid surface facing ventrolaterally is ornamented with muscle scars, and was probably the major area for insertion of muscles which move the head and neck (Figs 12 and 17).

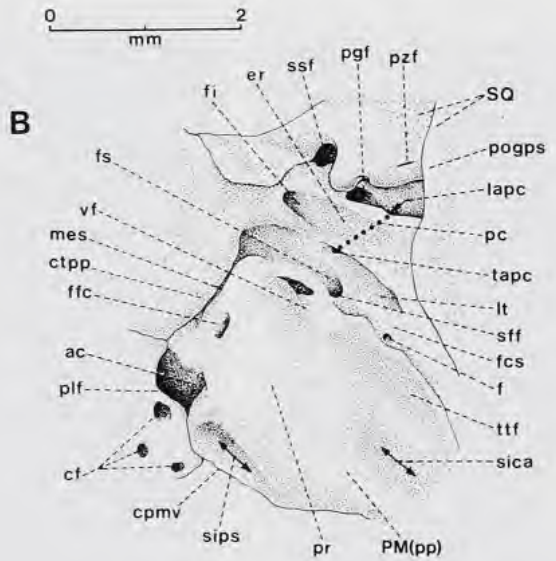
Viewed ventrally (Fig. 19) the pars mastoidea contributes posteromedially to the formation of the lateral half of the very small exoccipital process and it forms all of the larger mastoid process laterally. The anteroventral rim at its medial-most edge is united with the pars petrosa by a narrow bridge of bone on the lateral side of the posterior lacerate foramen. Lateral to this bridge, the anteroventral rim of the pars mastoidea forms an anteriorly directed lip which represents the caudal tympanic process of the petromastoid (*sensu* WIBLE, 1990). It underhangs a fossa located between it and the posterior end of the promontorium of the pars petrosa which is called the mastoid epitympanic sinus (*sensu* ARCHER, 1976a: 314). Lateral to the caudal tympanic process of the petromastoid, is the well developed mastoid process, and along its lateral and medial surfaces anteriorly is the stylomastoid notch, through which the facial nerve and lateral head vein leave the middle ear (WIBLE, 1990). The lateral extremity of the anteroventral rim of the pars mastoidea extends anterodorsally, up to the medial border of the fossa incudis at the posteromedial extremity of the epitympanic recess, lateral to the fenestra vestibuli.

The pars petrosa, viewed ventrally, is dominated by a large teardrop-shaped promontorium (=pars cochlearis) which is broadest posteriorly and tapers anteromedially to a point at the junction of the alisphenoid-basisphenoid-basioccipital. In lateral view the ventral border of the promontorium is at a level slightly dorsal to the ventral edge of the dorsal occipital condyles. The ventral surface of the promontorium is nearly smooth and the minor topographic variations largely reflect turns of the cochlear duct.

Anteriorly, a broad shallow depression is located between the promontorium and the large foramen ovale; it begins at the anteromedial edge of the large ovoid bulge of the promontorium, extends anterior and parallel to the basioccipital suture, crosses onto the alisphenoid just lateral to the medial lacerate foramen, and passes on the alisphenoid, to the posterior edge of the entocarotid foramen. This depression marks the route of passage of the internal carotid artery (i.e. sulcus for internal carotid artery) on its way to the entocarotid foramen; the passage of the internal carotid artery is thus situated medially (*sensu* PRESLEY, 1979). The large fossa lateral to this depression on the anterolateral surface of the promontorium is for insertion of the tensor tympani muscle. The medial edge of the promontorium parallel and adjacent to the basioccipital suture is elevated and rounded, a feature produced by the internal sulcus for the inferior petrosal sinus which exits the basicranium through the inferior petrosal foramen at the posteromedial edge of the promontorium.

Source : MNHN, Paris





Source : MNHN, Paris

Two openings occur on the posterior surface of the promontorium. The first and smallest is the fenestra cochleae which is situated on the posterolateral surface of the promontory anterolateral to the lateral edge of the posterior lacerate foramen and opens laterally; it occurs at the ventral edge of a shallow depression, the fossula fenestra cochleae. Viewed posteriorly, this fenestra occurs immediately anterior to the small exoccipital process at the exoccipital-pars mastoidea suture, and its ventral opening is at about the same level as the medial part of the ventral rim of the pars mastoidea (i.e. the lowest point of the trough separating the exoccipital and mastoid processes). The second and larger opening is the fenestra vestibuli which accommodates the footplate of the stapes and annular ligament; it has an ovoid (anteroposteriorly elongate) shape, a length/width ratio of 1.4 based on two specimens, and occurs dorsally on the lateral surface of the promontorium within a shallow depression, the vestibular fossula. In lateral view, this fenestra is seen at the posterodorsal edge of the external acoustic meatus. It thus lies anterolateral and a little dorsal to the fenestra cochleae, and the two fenestra are separated by a broadly rounded and vertically oriented swelling of the posterolateral corner of the promontorium.

FIG. 19. — *Pucadelphys andinus*. A, reconstruction of the right side of the basicranium in ventral view, based on YPFB Pal 6105 (holotype) and 6110; B, right ear region in ventral view (YPFB Pal 6110). The foramen ovale is restored. Abbreviations: **ac**, aquaeductus cochleae; **al**, anterior lamina; **AS**, alisphenoid; **BO**, basioccipital; **BS**, basisphenoid; **cf**, condyloid foramen; **cpmv**, crista promontorii medioventralis; **ctpp**, caudal tympanic process of pars mastoidea of petromastoid; **doc**, dorsal occipital condyle; **eam**, external acoustic meatus; **ef**, entocarotid foramen (=anterior carotid foramen, carotid canal); **EO**, exoccipital; **eop**, exoccipital process; **er**, epitympanic recess; **f**, foramen; **fc**, fenestra cochleae (=rotunda); **fcs**, floor of cavum supracochleare; **ffc**, fossula fenestra cochleae; **fi**, fossa incudis; **fo**, foramen ovale; **frcm**, fossa for rectus capitis muscle; **fs**, facial sulcus; **fstm**, fossa for stapedial muscle; **fv**, fenestra vestibuli (=ovalis); **gf**, glenoid fossa; **icf**, intercondylar fossa; **ipf**, inferior petrosal foramen (=internal jugular foramen); **lapc**, lateral aperture of prootic canal; **lt**, lateral trough; **mes**, mastoid epitympanic sinus of epitympanic recess; **mlf**, median lacerate foramen; **mp**, mastoid process; **pc**, prootic canal; **pgf**, postglenoid foramen; **plf**, posterior lacerate foramen (=jugular foramen); **PM(pm)**, pars mastoidea of petromastoid (=mastoid s.s.); **PM(pp)**, pars petrosa of petromastoid (=petrosal s.s.); **pogps**, postglenoid process of squamosal; **pr**, promontorium of pars petrosa of petromastoid; **ptp**, posttympanic process; **pzf**, postzygomatic foramen; **sff**, secondary facial foramen; **sica**, sulcus for internal carotid artery; **sips**, sulcus for inferior petrosal sinus; **smn**, stylomastoid notch; **SQ**, squamosal; **ssf**, subsquamosal foramen (=suprameatal, postsquamosal); **tapc**, tympanic aperture of prootic canal; **ttf**, tensor tympani fossa; **vf**, vestibular fossula; **voc**, ventral occipital condyle.

FIG. 19. — Pucadelphys andinus. A, *Reconstitution du côté droit de la base du crâne en vue ventrale d'après YPFB Pal 6105 (holotype) et 6110; B, vue ventrale de la région auditive droite (YPFB Pal 6110). Le foramen ovale est reconstitué. Abréviations:* ***ac****, aqueduc cochléaire;* ***al****, lame antérieure;* ***AS****, alisphénoïde;* ***BO****, basioccipital;* ***BS****, basisphénoïde;* ***cf****, foramen condylien;* ***cpmv****, crista promontorii medioventralis;* ***ctpp****, processus tympanique caudal de la pars mastoidea du pétromastoïde;* ***doc****, condyle occipital dorsal;* ***eam****, méat acoustique externe;* ***ef****, foramen entocarotidien (=foramen carotidien antérieur, canal carotidien);* ***EO****, exoccipital;* ***eop****, processus exoccipital;* ***er****, recessus épitympanique;* ***f****, foramen;* ***fc****, fenestra cochleae (=rotunda);* ***fcs****, plancher du cavum supracochleare;* ***ffc****, fossula fenestra cochleae;* ***fi****, fossa incudis;* ***fo****, foramen ovale;* ***frcm****, fosse pour le muscle rectus capitis;* ***fs****, sillon facial;* ***fstm****, fosse pour le muscle stapédial;* ***fv****, fenestra vestibuli (=ovalis);* ***gf****, fosse glénoïde;* ***icf****, fosse intercondylienne;* ***ipf****, foramen pétreux inférieur (=foramen jugulaire interne);* ***lapc****, ouverture latérale du canal prootique;* ***lt****, dépression latérale;* ***mes****, sinus épitympanique mastoïde du recessus épitympanique;* ***mlf****, trou déchiré moyen;* ***mp****, processus mastoïde;* ***pc****, canal prootique;* ***pgf****, foramen postglénoïde;* ***plf****, trou déchiré postérieur (=foramen jugulaire);* ***PM(pm)****, pars mastoidea du pétromastoïde (=mastoïde s.s.);* ***PM(pp)****, pars petrosa du pétromastoïde (=pétreux s.s.);* ***pogps****, processus postglénoïde du squamosal;* ***pr****, promontoire de la pars petrosa du pétromastoïde;* ***ptp****, processus posttympanique;* ***pzf****, foramen postzygomatique;* ***sff****, foramen facial secondaire;* ***sica****, sillon pour la carotide interne;* ***sips****, sillon pour le sinus prétreux inférieur;* ***smn****, échancrure stylomastoïdienne;* ***SQ****, squamosal;* ***ssf****, foramen subsquamosal (=supraméatal, postsquamosal);* ***tapc****, ouverture tympanique du canal prootique;* ***ttf****, fosse pour le muscle tensor tympani;* ***vf****, fossette vestibulaire;* ***voc****, condyle occipital ventral.*

Source : MNHN, Paris

A large ovoid secondary facial foramen, which is the opening of the facial nerve (VII) canal into the middle ear, occurs just anterior to the dorsal edge of the fenestra vestibuli. The secondary facial foramen opens posteriorly and a sulcus for the facial nerve (sulcus facialis) occurs immediately posterior to this foramen and separates the fenestra vestibuli from the epitympanic recess and the lateral trough (see below); these features are clearly seen in YPFB Pal 6110 (Fig. 19).

The epitypanic recess is "the extension of the middle ear cavity that lies dorsal to the tympanic membrane and contains the mallear-incudal articulation" (WIBLE, 1990: 188), (see also VAN DER KLAAUW, 1931: 73; and ARCHER, 1976a: 226). It is also called the fossa capitis mallei. The posterior extremity of the epitympanic recess is a deep and narrow pit where the ligament of the crus breve of the incus attaches: it is the fossa incudis or fossa crus breve incudis. In *Pucadelphys*, the epitympanic recess is an oblique, slightly concave depression in the roof of the tympanic cavity, approximately three times longer than wide, and bordered laterally and medially by thin bony rims. It is limited anteriorly by the squamosal at the anterior edge of the postglenoid foramen. The lateral rim of the epitympanic recess forms the medial wall of the postglenoid foramen (this is clearly seen on the right side of YPFB Pal 6110).The fossa incudis is a small pit located at the posteromedial extremity of the epitypanic recess.

The lateral trough is a well developed anteroposteriorly elongate slit that opens medially just lateral to the secondary facial foramen. It is formed by a depression in the petromastoid overhanging the medial rim of the epitympanic recess as clearly seen on the right side of YPFB Pal 6110 (Fig. 19). In the posterior end of the lateral trough is a small foramen which represents the tympanic aperture of the prootic canal which connects the lateral head vein (vena capitis lateralis; ARCHER, 1976a: 302; WIBLE, 1990) to the prootic sinus (Fig. 19). The prootic canal has a lateral opening within the petromastoid (lateral aperture of prootic canal) into the postglenoid canal (as seen on left side of YPFB Pal 6110) where the lateral head vein joins with the prootic sinus at its juncture with the sphenoparietal emissary vein (Fig. 21).

A small fossa for the origin of the stapedius muscle (fossa stapedius or fossa muscularis minor) occurs on the medial side of the lateral part of the stylomastoid notch and dorsal to it, just posterolateral to the fenestra vestibuli, posterior to the sulcus for the facial nerve. The fossa is shallow, dorsoventrally elongated, and faces medially. It is backed on to the fossa incudis (Fig. 19).

A tiny anteriorly directed opening foramen occurs on the lateral side of the fossa for the tensor tympani muscle, adjacent to the promontorium between the secondary facial foramen and the foramen ovale (Fig. 19). This foramen leads into a passage which joins with the posterior end of the facial canal within the petromastoid.

Two tiny openings occur in the posteromedial wall of the petromastoid, within the posterior lacerate foramen, which connect with the vestibular cavity (Figs 19, 21). The first is the aquaeductus cochleae which transmits the perilymphatic duct and a vein; it is situated in a vertical sulcus just dorsal to the outer opening of the posterior lacerate foramen within the jugular sulcus, on the medial side of the bridge joining the pars mastoidea and pars petrosa. Viewed posteriorly this opening is at about the same level as the dorsal rim of the fenestra cochleae. The second

Source : MNHN, Paris

opening is the aquaeductus vestibuli which transmits a vein and the endolymphatic duct. It is a small vertical slit deep within the posterior lacerate foramen, dorsal to the aquaeductus cochleae, on the anterior side of the jugular sulcus at a level corresponding to the lower edge of the subarcuate fossa posterior to the crus commune (Fig. 21); it opens posteriorly on the back surface of the broad crista separating the subarcuate fossa and jugular sulcus.

The cerebellar surface of the petromastoid consists principally of a large broadly ovoid central body oriented dorsolaterally-ventromedially, with two large openings (Fig. 21). The first opening, the subarcuate fossa, is the more dorsoposterior of the two and is a deep spheroidal pocket which opens medially; it houses the paraflocculus of the cerebellum. The second opening, the internal acoustic meatus, is more ventromedially located and is separated from the subarcuate fossa by a broad horizontally oriented septum of which the posteromedial part is the crus commune. The internal acoustic meatus is a broad shallow opening containing two deeper pits separated by a low transverse septum. The larger of these pits is the foramen acusticum inferius which is set posteromedial to the other and serves for transmitting two branches of the vestibulocochlear nerve (VIII); it has a fusiform shape and opens dorsomedially. The smaller of the pits is the foramen acusticum superius which is set anterolateral to the first and is a vertical slit which opens posteromedially and a little ventrally; it transmits the facial (VII) and branches of the vestibulocochlear (VIII) nerves. The ventral rim of the internal acoustic meatus opens onto a large anteromedially projecting platform, which is rounded and thickened anteriorly to form a divide which separates, on the one hand a broad medially directed sulcus leading from the foramen acusticum inferius on its posterior side, and on the other hand a smaller more anteriorly directed and dorsally situated sulcus running from the foramen acusticum superius on its anterior side.

FIG. 20. — *Pucadelphys andinus*. View of the cerebellar (dorsomedial) surface of petromastoid of YPFB Pal 6470. Stereophotos, X 5.

FIG. 20. — Pucadelphys andinus. *Vue de la surface cérébellaire (dorso-médiale) du pétromastoïde de YPFB Pal 6470. Photos stéréoscopiques, X 5.*

Source : MNHN, Paris

Four principal sulci surround the central body of the petromastoid on its cerebellar surface (Fig. 21): 1) Along the ventromedial edge is an elongate sulcus for the inferior petrosal sinus which is bordered dorsally by the crista promontorii medioventralis. This sinus connects "the venous sinus (sinus cavernosus) encasing the pituitary gland and optic chiasma with the internal jugular vein just before it emerges from the inferior petrosal foramen" (MACINTYRE, 1972: 291). 2) Posteroventrally, is a shallow and nearly vertical sulcus for the jugular sinus. 3) Posterodorsally is a small pocket representing the sulcus for the sigmoid sinus. A tiny medially opening foramen in the deepest part of this sinus extends laterally and apparently connects with the canal from the small foramen in the dorsoposterior end of the sulcus for the prootic sinus (see below). There is also the cerebellar opening of the mastoid foramen for the occipital emissary vein. 4) Along the dorsolateral edge is an elongate sulcus for the prootic sinus, a primary tributary of the lateral head vein, which is walled by the squamosal laterally and by a crest of the petromastoid medially.

Anterolaterally to the crista petrosa is a large depression in an anterdorsally projecting wing of the petromastoid for part of the temporal lobe of the cerebrum and the trigeminal (=gasserian or semilunar) ganglion of the trigeminal nerve (V). In other didelphids the trigeminal ganglion lays on the alisphenoid and no anterodorsally projecting wing is observed. At the anteromedial edge of this depression along the lateral surface of the crista petrosa is a small foramen which opens anteromedially into a groove (seen clearly in YPFB Pal 6107 and 6470); this is the hiatus Fallopii which transmits the greater petrosal nerve, a branch of the facial nerve (VII). The anterolateral wing makes an extensive contribution to the floor of the middle cranial fossa (Fig. 21) and the internal side of the lateral wall of the braincase (the lateral side is formed by the squamosal and the alisphenoid; it apparently represents the relic of a reduced anterior lamina of the petrosal (*sensu* CROMPTON & JENKINS, 1979: 71, figs 3-5B, C) (see below for justification and discussion). In ventral view, an irregular contact is clearly seen between the anterolateral border of the promontorium and the flat shelf which forms the posterior edge of the foramen ovale in YPFB Pal 6105 (Fig. 19). This portion probably represents part of the anterior lamina. The anterior lamina is covered laterally by the squamosal and the alisphenoid. Its uncovered portion, visible in ventral view of the skull, lies medial to the squamosal. It forms the posterior rim of the foramen ovale, extending from the squamosal suture laterally across the anterior surface of the promontorium as a broad uneven ledge to the alisphenoid contact lateral to the medial lacerate foramen.

On the lateral (squamosal) side of the petromastoid (Fig. 21) is a broad shallow anteroventrally directed sulcus which transmitted the prootic sinus along its greater length and the sphenoparietal emissary vein ventrally. The lateral aperture of the prootic canal occurs at the anteroventral end of this sulcus and this aperture approximates the boundary between the prootic sinus (dorsally) and sphenoparietal emissary vein (ventrally). A small anteriorly directed opening foramen occurs dorsally on the petromastoid, just posterior to the sulcus for the prootic sinus. This foramen transmits a branch of the prootic sinus posteriorly within the pars mastoidea, and the canal apparently unites medially with the small foramen in the dorsal end of the sigmoid sinus (Fig. 21). A small shallow sulcus unites this foramen with the dorsoposterior edge of the sulcus for the prootic sinus (Fig. 21).

Source : MNHN, Paris

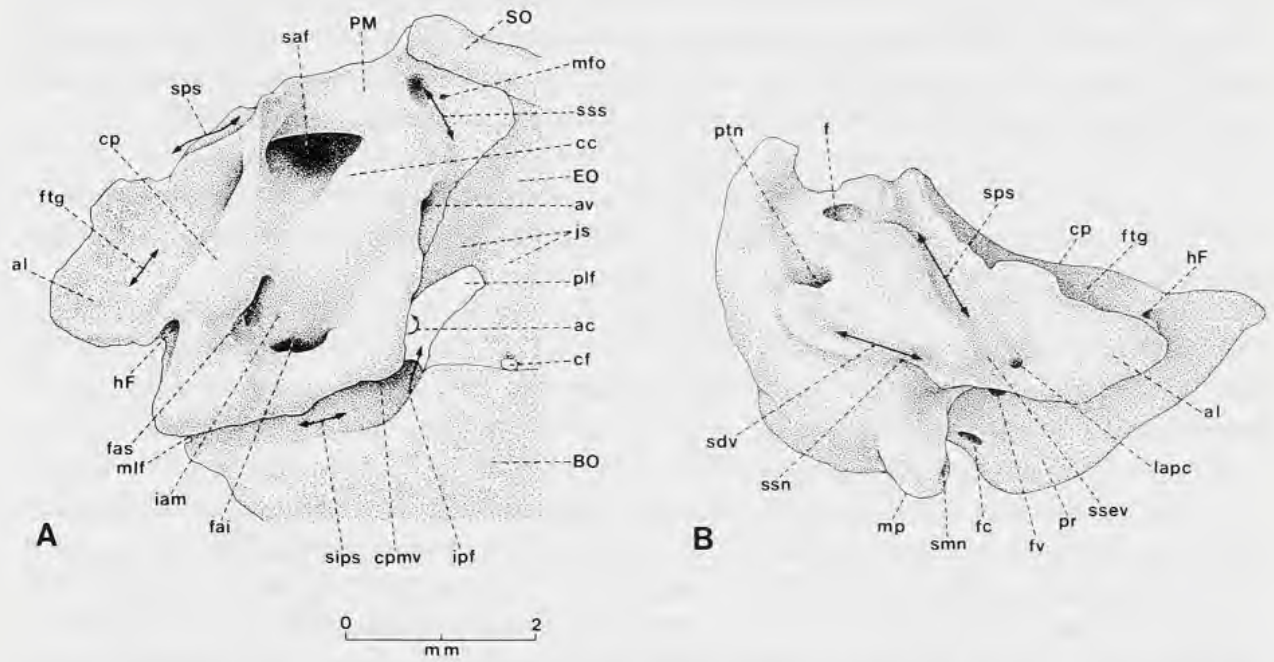


FIG. 21. — *Pucadelphys andinus*. Details of petromastoid (A, cerebellar or dorsomedial surface; B, squamosal or lateral surface), based on YPFB Pal 6470. Abbreviations: **ac**, aquaeductus cochleae; **al**, anterior lamina; **av**, aquaeductus vestibuli (=endolymphatic foramen); **BO**, basioccipital; **cc**, crus commune; **cf**, condyloid foramen; **cp**, crista petrosa; **cpmv**, crista promontorii medioventralis; **EO**, exoccipital; **f**, foramen; **fai**, foramen acusticum inferius (=area cochleae); **fas**, foramen acusticum superius (=area facialis); **fc**, fenestra cochleae (=rotunda); **ftg**, fossa for trigeminal ganglion; **fv**, fenestra vestibuli (=ovalis); **hF**, hiatus Fallopii; **iam**, internal acoustic meatus; **ipf**, inferior petrosal foramen (=internal jugular foramen); **js**, jugular sulcus; **lapc**, lateral aperture of prootic canal; **mfo**, mastoid foramen; **mlf**, median lacerate foramen; **mp**, mastoid process; **plf**, posterior lacerate foramen (=jugular foramen); **PM**, petromastoid; **pr**, promontorium of pars petrosa of petromastoid; **ptn**, posttemporal notch; **saf**, subarcuate fossa (=floccular, parafloccular fossa); **sdv**, sulcus for diploetic vessels; **sips**, sulcus for inferior petrosal sinus; **smn**, stylomastoid notch; **SO**, supraoccipital; **sps**, sulcus for prootic sinus; **SQ**, squamosal; **ssev**, sulcus for sphenoparietal emissary vein; **ssn**, subsquamosal notch; **sss**, sulcus for sigmoid sinus; **tapc**, tympanic aperture of prootic canal; **ttf**, tensor tympani fossa.

FIG. 21. — Pucadelphys andinus. *Détails du pétromastoïde (A, face cérébellaire ou dorso-médiale; B, face squamosale ou latérale), d'après YPFB Pal 6470. Abréviations:* ***ac****, aquaeductus cochleae;* ***al****, lame antérieure;* ***av****, aquaeductus vestibuli (=foramen endolymphatique);* ***BO****, basioccipital;* ***cc****, crus commune;* ***cf****, foramen condylien;* ***cp****, crista petrosa;* ***cpmv****, crista promontorii medioventralis;* ***EO****, exoccipital;* ***f****, foramen;* ***fai****, foramen acusticum inferius (=area cochleae);* ***fas****, foramen acusticum superius (=area facialis);* ***fc****, fenestra cochleae (=rotunda);* ***ftg****, fosse pour le ganglion trigeminal;* ***fv****, fenestra vestibuli (=ovalis);* ***hF****, hiatus Fallopii;* ***iam****, méat auditif interne;* ***ipf****, foramen pétreux inférieur (=foramen jugulaire interne);* ***js****, sillon jugulaire;* ***lapc****, ouverture latérale du canal prootique;* ***mfo****, foramen mastoïde;* ***mlf****, trou déchiré moyen;* ***mp****, processus mastoïde;* ***plf****, trou déchiré postérieur (=foramen jugulaire);* ***PM****, pétromastoïde;* ***pr****, promontoire de la pars petrosa du pétromastoïde;* ***ptn****, échancrure posttemporale;* ***saf****, fossa subarcuata (= fosse flocculaire ou parafloculaire);* ***sdv****, sillon pour les vaisseaux diploetiques;* ***sips****, sillon pour le sinus pétreux inférieur;* ***smn****, échancrure stylomastoïdienne;* ***SO****, supraoccipital;* ***sps****, sillon pour le sinus prootique;* ***SQ****, squamosal;* ***ssev****, sillon pour la veine émissaire sphénopariétale;* ***ssn****, échancrure subsquamosale;* ***sss****, sillon pour le sinus sigmoïde;* ***tapc****, ouverture tympanique du canal prootique;* ***ttf****, fosse pour le muscle tensor tympani.*

A less well defined sulcus extends posteriorly from the sulcus for the sphenoparietal emissary vein along the ventral edge of the pars mastoidea, then bends dorsoposteriorly. This sulcus apparently transmitted the arteria diploetica magna and vena diploetica magna (*sensu*

Source : MNHN, Paris

WIBLE, 1990) which passed through the posttemporal foramen at the posttemporal notch. The vena diploetica magna united with the sphenoparietal emissary vein at a point level with the lateral aperture of the prootic canal. The sphenoparietal emissary vein and arteria diploetica magna passed ventrally and exited the skull through the postglenoid foramen (WIBLE, 1990).

ECTOTYMPANIC. — There is no evidence of an ossified ectotympanic (the bone which supports the tympanic membrane) nor are there facets in the ear region which marked the site of attachment of this bone.

DISCUSSION

The comparison of the skulls of *Pucadelphys andinus* is difficult in spite of the good preservation of the remains. As a matter of fact, there is no described skull of fossil marsupials from the Cretaceous, and the skull of *Mayulestes ferox* from the early Paleocene of Tiupampa, with which *P. andinus* could reasonably be compared, is only known by a preliminary description (MUIZON, 1994) and its thorough study is under progress by one of us (C. M.). However, two undescribed probable metatherian skulls from the late Cretaceous of Mongolia have been mentioned in the litterature. KIELAN-JAWOROWSKA & NESSOV (1990) referred to the Metatheria a complete deltatheroidan skull well known as the Gurlin Tsav Skull and TROFIMOV & SZALAY (1993) mentioned the skeleton of a *Monodelphis scalops*-sized Asiadelphia from the Barun Goyot Formation of Mongolia. Another specimen, known from the middle Paleocene of São José de Itaboraí (Brazil), belongs to a polydolopid and consequently cannot be used for a comparison with a didelphid; furthermore, its very poor state of preservation does not permit reasonable comparisons. However, several well preserved skulls (or partial skulls) of primitive mammals are known from the Jurassic and the Cretaceous. The most important are: morganucodontids [*Morganucodon*, (KERMACK, 1963; and KERMACK *et al.*, 1981)], *Gobiconodon* (JENKINS & SCHAFF, 1988), *Sinoconodon* (CROMPTON & LUO, 1993), docodonts [*Haldanodon* (LILLEGRAVEN & KRUSAT, 1991)], several multituberculates, [among others: *Kamptobaatar* and *Sloanbaatar* (KIELAN-JAWOROWSKA, 1971), *Catopsbaatar* and *Chulsanbaatar* (KIELAN-JAWOROWSKA, 1974), *Catopsalis* (KIELAN-JAWOROWSKA & SLOAN, 1974), *Kryptobaatar* and *Tugrigbaatar* (KIELAN-JAWOROWSKA & DASHZEVEG, 1978), *Nemegtbaatar*, (KIELAN-JAWOROWSKA *et al.*, 1986)], eupantotheres [*Vincelestes* (BONAPARTE & ROUGIER, 1987; ROUGIER & BONAPARTE, 1988; ROUGIER *et al.*, 1992; and HOPSON & ROUGIER, 1993)], deltatheroidans [*Deltatheridium* (KIELAN-JAWOROWSKA, 1975: a partial skull only) and the Gurlin Tsav skull, (KIELAN-JAWOROWSKA & NESSOV, 1990)], and eutherians [*Asioryctes*, *Barunlestes*, *Kennalestes* and *Zalambdalestes* (KIELAN-JAWOROWSKA, 1981; 1984; KIELAN-JAWOROWSKA & TROFIMOV, 1980)]. Although not directly related to *Pucadelphys* they are extremely useful for determining the primitive features of the genus. The skulls of Tiupampa (*Pucadelphys* and *Mayulestes*) are the oldest known undoubted marsupial skulls and, in the future, they will represent the best sample for the study of primitive marsupials. *Pucadelphys* is also one of the oldest known didelphids and its teeth can be compared with the abundant dental remains from the "middle"

Source : MNHN, Paris

Paleocene of Itaboraí which were revised by MARSHALL (1987). Consequently, the discussion will be divided into two sections. The first section will compare the teeth of *Pucadelphys* to those of the Paleocene didelphids of Itaboraí and of the late Cretaceous marsupial dental remains of North America related to the *Alphadon* group. The second section will consider the major cranial characters of *Pucadelphys* and, by comparing them to the available skulls of Mesozoic mammals, we will try to determine their phylogenetic state and polarity.

DENTAL COMPARISON. — Among all the fossil didelphids known in the lower Tertiary of South America, *Sternbergia itaboraiensis* from the middle Paleocene (Itaboraian) of São José de Itaboraí (Brazil) is the closest to *P. andinus* with respect to size as well as to tooth structure. Both species possess, among other features, the same didelphid characters, which are the paracone smaller than the metacone and the V-shaped centrocrista. The affinities of the two forms were noted since the first discoveries at Tiupampa by MUIZON *et al.* (1984) who described a tooth that they related to a "*Sternbergia*-like" marsupial and that must now be referred to *P. andinus*. *Sternbergia itaboraiensis* was described by PAULA COUTO (1970) on the basis of a mandible fragment with m4 and the talonid of m3. A revision of *S. itaboraiensis* was provided by MARSHALL (1987) who included in the hypodigm of the species several other specimens of the lower and upper dentition. With the exception of their dental structure, which is almost identical, *P. andinus* and *S. itaboraiensis* share the same morphology of the protocone, which is long anteroposteriorly, triangular-shaped, and inflated posteriorly, and the important development of the styles B and C. However, the two species clearly differ in the different development of several of their elements. The upper molars of *Sternbergia* differ from those of *Pucadelphys* in their shallower trigon basin, in their more reduced paracone, in their more deeply V-shaped centrocrista, in their smaller conules, in their smaller stylar shelf with a shallower basin, in the reduction of the style A which does not form a parastyle as large as in *Pucadelphys*, in their very reduced style D (while it is often the same size as style C or larger in *Pucadelphys*), in the reduction of the metacone of their M4 which is fused to the posterolabial angle of the tooth, in the loss of the posterior part of the stylar shelf basin of M4 and in the great anterolabial projection of the parastylar region of the stylar shelf of M4 with a larger paracrista. The lower molars of *Sternbergia* differ from those of *Pucadelphys* in that the talonids of m3 and m4 are always wider than the trigonids (in *Pucadelphys* the talonid of these teeth is sometimes as wide as the trigonid but is often narrower), in the anteroposteriorly longer trigonid, in the lower and stouter trigonid cusps, in that the metaconid and paraconid are more separated one from the other, a condition which more widely opens the trigonid basin lingually, in the hypoconid which has a better marked V-shaped morphology, in the larger hypoconulid and entoconid and in the presence of well developed anterior and labial cingula (they are absent in *Pucadelphys*). Most of the dental characters of *Pucadelphys* are more primitive than those of *Sternbergia* and, as already expressed by MARSHALL & MUIZON (1988) and MUIZON (1992), the former represents a good morphological ancestor for the latter, as far as the teeth are concerned.

Two other marsupials from Itaboraí share structural similarities with *Pucadelphys andinus*; they are *Marmosopsis juradoi* PAULA COUTO (1962) and *Itaboraidelphys camposi* MARSHALL & MUIZON (1984).

Source : MNHN, Paris

M. juradoi is known by several upper and lower jaws and its hypodigm has been revised by MARSHALL (1987). It differs from *P. andinus* in its smaller size, its upper molars proportionally slightly narrower and longer and its molar cusps sharper and less bulky. In comparison to those of *Pucadelphys*, the upper molars of *Marmosopsis* differ in having a higher metacone relative to the paracone, a smaller protocone, a shorter and straight preprotocrista, smaller conules, a shallower stylar shelf basin, a much higher metacrista which is straight in occlusal and anterior views (it is concave in *Pucadelphys*), a slightly shorter paracrista, reduced styles C, D, and E. The lower molars of *Marmosopsis* have a higher trigonid (relatively to the talonid) with a smaller and lower paraconid, a shorter talonid with a smaller and shallower basin, a crest-like entoconid which links the hypoconulid to the posterior edge of the metaconid (in *Pucadephys* and *Sternbergia* a distinct entoconid is present) and the loss of a distinct hypoconid on m4. *Marmosopsis* differs from *Sternbergia* and resembles *Pucadelphys* in having a relatively little marked V-shaped centrocrista (a primitive feature); however, it differs from both genera in having a very large and straight metacrista, in the crest-like entoconid, and in the reduction of the talonid of the m4 which has no hypoconid. MARSHALL & MUIZON (1988) and MUIZON (1992) have suggested that *Mizquedelphys* from the early Paleocene of Tiupampa could represent a possible morphological ancestor for *Marmosopsis*, as far as the teeth are concerned.

The molars of *Itaboraidelphys camposi* are also structurally similar to those of *Pucadelphys andinus* but differ from them in their size, approximately 50% larger, in their more robust morphology and in their lower and stouter cusps. The upper molars of *Itaboraidelphys* differ from those of *Pucadelphys* in being transversally narrower, in the more pronounced V-shaped centrocrista, in the larger conules, in the smaller style C which is clearly closer in size to style B than D and is sometimes twinned, and in the larger and straighter metacrista in occlusal view. The lower molars of *Itaboraidelphys* differ from those of *Pucadelphys* in their higher trigonid (relative to the talonid) which is more open lingually, in the shallower trigonid and talonid basins, in the stronger anterocingulid, in the shorter talonid and in the smaller hypoconulid. MARSHALL & MUIZON (1988) and MUIZON (1992) have stated that *Andinodelphys* from the early Paleocene of Tiupampa could represent a possible morphological ancestor for *Itaboraidelphys*, although MARSHALL *et al.* (1989) regard it as a plesion of indeterminate familial attribution which could be related to the origin of the Australian marsupials.

It is true that *Marmosopsis* and *Itaboraidelphys* differ more from *Pucadelphys* than does *Sternbergia,* which is the reason why we have suggested a closer relationship between the latter two (MARSHALL & MUIZON, 1988; MUIZON, 1992). However, there is apparently no feature that could exclude *Pucadelphys* from being a possible ancestor of *Marmosopsis* and *Itaboraidelphys,* as the principal derived features of *Pucadelphys* are the V-shaped centrocrista and the larger and higher metacone relatively to the paracone, two didelphid characters.

Pucadelphys also shows dental similarities with the various species of *Alphadon* and *Protalphadon* of the late Cretaceous of North America, which were classified in the family Peradectidae by MARSHALL *et al.* (1989). The three genera present a similar dental structure with large styles A to D, but *Pucadelphys* differs from the other two genera in possessing a V-shaped centrocrista (straight in *Alphadon* and *Protalphadon*), a paracone smaller than the metacone (they

Source : MNHN, Paris

are subequal in size in *Alphadon* and *Protalphadon*) and an inflated posterior base of the protocone, which are didelphid characters. CLEMENS (1966) has suggested that the Tertiary didelphids were structurally similar to species like *Alphadon lulli* and *Alphadon marshi*. As a matter of fact, *Alphadon marshi* represents a good structural ancestor for the dental morphology of *Pucadelphys andinus*, an observation which confirms the hypothesis of CLEMENS (1966), CROCHET (1980) and REIG *et al.* (1987) which states that the Didelphidae may have originated from the North American Peradectidae. It is noteworthy that some specimens of *Alphadon marshi* (from the Maastrichtian of the Scollard Formation, Alberta, Canada) have a slightly V-shaped centrocrista and a paracone smaller than the metacone (CIFELLI, 1990: 315); the same has been observed by SAHNI (1972: 383 and fig. 14p) in a molar referred to *Alphadon* cf. *rhaister* from the Campanian of Judith River Formation (Montana). However, when present, these features are generally less developed than in the Didelphidae.

CHARACTER ANALYSIS. — In this section we analyze character states in *Pucadelphys* which are of potential importance in phylogenetic inference. This analysis is made in order to determine which states are plesiomorphic or apomorphic for Metatheria in particular and Tribosphenida in general. The relevance of these states for the phylogenetic relationships of *Pucadelphys* are summarized in the conclusions below. The character states are discussed in the following order: dentition, dentary, skull bones, skull foramina, and ear region (petromastoid).

DENTITION

Number of incisors. — HERSHKOVITZ (1982) has shown that the ancestral metatherian (and probably eutherian) primitively had five upper and lower incisors, although the highest number known is 5/4 which resulted from the loss of i1. Therefore, so far, the plesiomorphic number of incisors for Tribosphenida and Metatheria is 5/4 (I1, I2, I3,I 4, I5/i2, i3, i4, i5) (MARSHALL, 1979; HERSHKOVITZ, 1982; CLEMENS & LILLEGRAVEN, 1986: 71). *Pucadelphys* thus retains the plesiomorphic state for Tribosphenida and Metatheria.

Structure of upper incisors. — The relative size and structure of metatherian upper incisors are discussed by TAKAHASHI (1974), ARCHER (1976b), and REIG *et al.* (1987). Metatheria were apparently plesiomorphic in having I1-5 conical in shape, while the spatulate shape as occurs in Microbiotheriidae and Australian taxa is the derived state (ARCHER, 1976b; REIG *et al.*, 1987). Many Didelphidae (TAKAHASHI, 1974) and Dasyuridae (ARCHER, 1976b) have the I1 hypsodont and semiprocumbent relative to I2, and a small space (diastema) separated I1 and I2. Archer (1976b) regarded both states as plesiomorphic for Metatheria, and HERSHKOVITZ (1982) suggested that these states evolved subsequent to loss of the i1 and are associated with grooming. Although both states occur in many generalized metatherians, some taxa have one state but not the other. In addition, *Dromiciops* has I1-5 equally spaced and I1 is not hypsodont (see REIG *et al.*, 1987, fig. 49) as also occurs in some Dasyuridae (ARCHER, 1976b, Table 1). The states in *Pucadelphys* in which I1-5 are conical, subequal in height and equally spaced (no diastema) are apparently

Source : MNHN, Paris

plesiomorphic for metatherians because it is possible to derive all the variations seen in Didelphidae, Dasyuridae, Microbiotheriidae and other groups from a *Pucadelphys*-like ancestor. The states in *Pucadelphys* probably also occurred in the ancestral tribosphenid.

Structure of lower incisors. — HERSHKOVITZ (1982) illustrated that all fossil metatherians except Microbiotheriidae have what he termed a staggered i3 (i.e. the second incisor of the four occurring in generalized metatherians) which has "a bony alveolar buttress on labial surface, greater root exposure on lingual surface and medially staggered position of root and alveolus" (p. 191). In addition, the staggered i3 is larger than the i2, i4 or i5. Given the nearly universal occurrence of this staggered i3 in metatherians, HERSHKOVITZ concluded that this state was plesiomorphic for this group. He also demonstrated that this state occurs in an edentulous dentary from the Albian of Texas (see his fig. 5) which places a minimum age for the metatherian-eutherian dichotomy. However, the lower incisors in *Pucadelphys* (YPFB Pal 6107), Microbiotheriidae (MARSHALL, 1982) and generalized eutherians (HERSHKOVITZ, 1982) are arranged in a linear series and have no staggered i3. This state was thus probably plesiomorphic for Tribosphenida and was retained in eutherians and in a few metatherians (*Pucadelphys*, Microbiotheriidae). The staggered i3 is here regarded as a derived state which appears to be synapomorphic for metatherians except *Pucadelphys* and Microbiotheriidae.

Number of premolars and molars. — The plesiomorphic number of permanent premolars and molars in Tribosphenida was probably P5/5 and M4/4, while loss of one molar would account for the plesiomorphic state in eutherians of P5/5 and M3/3 and loss of two premolars for the plesiomorphic state in metatherians of P3/3 and M4/4 (DASHZEVEG & KIELAN-JAWOROWSKA, 1984, pp. 225-226). The loss of deciduous incisors, canines and premolars (only the P3/3 has a predecessor, the HDP 3/3) is also a derived state for metatherians (ARCHER *et al.*, 1985). *Pucadelphys* thus retains the plesiomorphic metatherian dental formula of P3/3 and M4/4.

Structure of premolars and molars. — The structure of the cheek teeth in generalized metatherians is discussed by ARCHER (1976b), REIG *et al.* (1987), MARSHALL (1987) and MARSHALL *et al.* (1989). Based on these studies, *Pucadelphys* has a cheek tooth structure which agrees perfectly with members of the family Didelphidae (i.e. paracone smaller and lower than metacone; V-shaped (dilambdodont) centrocrista; well developed stylar shelf with large stylar cusps A, B, C and D; posteriorly expanded protoconal base; trigonid shorter than talonid; cristid obliqua contacts posterior wall of trigonid labial to protocristid notch; entoconid tall and spire-like; hypoconulid lower than entoconid; well developed pre- and postcingulids). The cheek tooth character states of Didelphidae relative to other metatherians are listed in MARSHALL *et al.* (1989, figs 1, 2).

Dentary

Inflected angular process. — The angular process of the dentary is strongly inflected medially in all metatherians except the living *Tarsipes* where it is absent, and in *Phascolarctos* and *Myrmecobius* where it is weakly developed. The angular process is inflected medially in most late Cretaceous eutherians from Asia (i.e. *Kennalestes*, *Asioryctes* and *Barunlestes*; KIELAN-

Source : MNHN, Paris

JAWOROWSKA, 1981, 1984; KIELAN-JAWOROWSKA *et al.*, 1979) and in some species of *Gypsonictops* and *Cimolestes* from North America, in Didymoconidae from the late Eocene-middle Oligocene of Asia, and in various groups of living and fossil rodents (MARSHALL, 1979 and references therein). One is also present in the early Cretaceous age pantothere *Vincelestes* from South America (BONAPARTE & ROUGIER, 1987) and in some triconodonts, symmetrodonts, and Multituberculata (MIAO, 1988: 878). The distribution of an inflected angular process suggests that it is a plesiomorphic state for Tribosphenida. *Pucadelphys* is thus plesiomorphous in this feature.

Mylohyoid groove. — The mylohyoid groove marks the course of a neurovascular bundle which includes the mylohyoid artery and nerve, and presumably in early taxa the persistent Meckel's cartilage (KREBS, 1971). It is present in Jurassic dryolestids (KREBS, 1971); in docodonts, triconodonts and eupantotheres (KIELAN-JAWOROWSKA, 1981: 61); in the early Cretaceous triconodont *Gobiconodon ostromi* (JENKINS & SCHAFF, 1988: 5); in the early therian *Kielantherium* (DASHZEVEG & KIELAN-JAWOROWSKA, 1984: 221); in the Cretaceous eutherians *Prokennalestes* and *Kennalestes* (KIELAN-JAWOROWSKA, 1981: 61 and KIELAN-JAWOROWSKA & DASHZEVEG, 1989); in some living adult eutherians [insectivorans, edentates, cetaceans; (BENSLEY, 1902)]; and in embryos of monotremes (WATSON, 1916). It is absent in multituberculates, some dryolestids (i.e. *Crusafontia*; KREBS, 1971), paurodontids (*Amphitherium*, *Peramus*); and some early eutherians (*Asioryctes*; KIELAN-JAWOROWSKA, 1981: 61). It is absent in the Deltatheroida (KIELAN-JAWOROWSKA & NESSOV, 1990), but present in *Pucadelphys*, embryos of some living marsupial taxa and, sporadically, in some adult specimens of *Didelphis*, *Trichosurus*, *Phalanger*, *Perameles* and *Petauroides* (BENSLEY, 1902). The presence of a mylohyoid groove is thus the plesiomorphic state for Mammalia, and *Pucadelphys* retains the primitive condition. The presence or absence of a mylohyoid groove appears (*contra* ARCHER *et al.*, 1985, fig. 3, point 14) to be of dubious value in phylogenetic inference.

Labial mandibular foramen. — KIELAN-JAWOROWSKA & DASHZEVEG (1989) named labial mandibular formen a small foramen on labial side of the dentary at the base of the coronoid process present in many primitive mammals. This small foramen occurs in *Kielantherium* (aegialodontid) from the early Cretaceous of Asia, in *Prokennalestes* (otlestid) from the Aptian-Albian of Asia, in *Otlestes* (otlestid) from the late Cenomanian of Uzbekistan and in *Zalambdalestes* (zalambdalestid) from the Campanian of Mongolia (DASHZEVEG & KIELAN-JAWOROWSKA, 1984; and KIELAN-JAWOROWSKA & DASHZEVEG, 1989), and in the microbiothere metatherian *Microbiotherium gallegosense* from the early Miocene of Argentina (MARSHALL, 1982). DASHZEVEG & KIELAN-JAWOROWSKA (1984) and KIELAN-JAWOROWSKA & DASHZEVEG (1989) regard the presence of this foramen as a therian plesiomorphy. There is no trace of this foramen in *Pucadelphys*.

BONES OF SKULL

There are numerous states in *Pucadelphys* which, as shown by previous workers, apparently represent Tribosphenida plesiomorphies. These include: nasals flared posteriorly (GREGORY, 1920: 139); alisphenoid and squamosal have major component in lateral wall of braincase (KERMACK *et al.*, 1981: 135; KEMP, 1982: 305, 1983: 372); glenoid fossa set posteriorly

Source : MNHN, Paris

opposite anterior half of promontorium (KIELAN-JAWOROWSKA, 1981: 65); occipital plate slopes upwards and slightly forwards from condyles (KIELAN-JAWOROWSKA, 1981: 65); and lambdoidal crest sharp, sagittal crest weak or absent (KIELAN-JAWOROWSKA *et al.*, 1979: 227).

Orbit large, confluent with temporal fossa. — This state occurs in *Vincelestes* (BONAPARTE & ROUGIER, 1987), Deltatheroida (KIELAN-JAWOROWSKA, 1975), *Zalambdalestes* (KIELAN -JAWOROWSKA, 1984: 113), *Asioryctes* and *Kennalestes* (KIELAN-JAWOROWSKA, 1981: 56), *Pucadelphys*, and in generalized Cenozoic and living metatherians and eutherians. This is apparently the plesiomorphic state for Theria.

Lacrimal. — The lacrimal has a large facial wing in cynodonts, *Morganucodon* (KERMACK *et al.*, 1981), *Vincelestes* (BONAPARTE & ROUGIER, 1987), *Deltatheridium* (KIELAN-JAWOROWSKA, 1975), *Pucadelphys* and in generalized living and fossil metatherians (GREGORY, 1920). In *Vincelestes*, *Deltatheridium*, *Pucadelphys* and in generalized living and fossil metatherians the lacrimal forms a prominent antorbital rim and the lacrimal foramen occurs within the orbital rim. The structure of the lacrimal and position of the lacrimal foramen in *Pucadelphys* apparently represents the plesiomorphic state for Tribosphenida.

Nasal-lacrimal contact.— A broad nasal-lacrimal contact occurs in cynodonts, tritylodontids, multituberculates, *Morganucodon* (KERMACK *et al.*, 1981), *Vincelestes* (BONAPARTE & ROUGIER, 1987, fig. 2A), *Deltatheridium* (Kielan-Jaworowska, 1975: 122, fig. 3A), and among metatherians only in South American Borhyaenoidea (MARSHALL, 1978; MARSHALL *et al.*, 1989) and in the Australian *Wynyardia* (GREGORY, 1920). A broad nasal-lacrimal contact is the plesiomorphic state for mammals (GREGORY, 1920). Living and other fossil metatherians (including *Pucadelphys*) are derived in having no nasal-lacrimal suture but a clear frontal-maxilla contact (GREGORY, 1920; MARSHALL & KIELAN-JAWOROWSKA, 1992). An intermediate condition within metatherians occurs in some Didelphidae (*Didelphis*, *Chironectes*) which have only a narrow and variable frontal-maxilla contact (GREGORY, 1920: 139). Most eutherians are also derived in having a broad frontal-maxilla contact (NOVACEK, 1986: 27).

Contact of alisphenoid and parietal. — A broad contact between the alisphenoid and parietal on the outside of the skull occurs in the early eutherians *Asioryctes* and *Kennalestes* (KIELAN-JAWOROWSKA, 1981), in *Pucadelphys*, and in many Cenozoic and living metatherians (i.e. all Didelphidae, Myrmecobiidae, most Dasyuridae, some Borhyaenoidea; ARCHER, 1976a: 309). There is no contact in Thylacinidae, Peramelidae, Vombatidae, some Phascolarctidae, some Borhyaenoidea, and some Dasyuridae (ARCHER, 1976a: 309). A broad alisphenoid-parietal contact is regarded as the plesiomorphic state in Tribosphenida.

Palate. — The bony palate is solid (without vacuities) in cynodonts, monotremes, some multituberculates (*Kamptobaatar*), the eupantothere *Vincelestes* (BONAPARTE & ROUGIER, 1987), the late Cretaceous eutherians *Zalambdalestes* (KIELAN-JAWOROWSKA, 1984: 108), most living and Cenozoic eutherians, the deltatheroidan *Deltatheridium* (KIELAN-JAWOROWSKA, 1975: 122), and many metatherians (Borhyaenoidea, *Sparassocynus*, *Caluromys*, *Dasycercus*, *Dasyuroides*, species groups of *Antechinus* and *Sminthopsis*, *Myrmecobius*, *Dactylopsila*, *Petaurus* and *Dactylonax*) (MARSHALL, 1979 and references therein). In contrast, the palate is perforated by large vacuities, often two pairs, in some multituberculates (i.e. *Sloanbaatar*, *Nemegtbaatar*,

Source : MNHN, Paris

Bulganbaatar and *Ptilodus*), some eutherians (rabbits, some rodents, macroscelidids, hedgehogs, *Carpolestes*), some Deltatheroida (KIELAN-JAWOROWSKA & NESSOV, 1990), and many living and fossil metatherians (MARSHALL, 1979; REIG *et al.*, 1987). Because of the wide occurrence of palatal vacuities among metatherians, their presence has generally been regarded as plesiomorphic for this group. However, when vacuities are present they are generally quite variable within families and even within species. Ontogenetic studies of metatherian embryos have shown that the palatal plates of the maxilla and palatine bones are at first solid and develop vacuities by gradual resorption of bone. These and other observations favor the view that a solid palate was the plesiomorphic state for mammals (MARSHALL, 1979 and references therein). *Pucadelphys* is thus plesiomorphic for this state.

Preglenoid process of jugal. — The jugal is deep, long and extends posteriorly to form a preglenoid process along the anterolateral edge of the glenoid fossa in the late Cretaceous metatherian *Didelphodon vorax* (CLEMENS, 1966: 72), in Cenozoic and living metatherians, in Deltatheroida (KIELAN-JAWOROWSKA & NESSOV, 1990), in the early Cretaceous eupantothere *Vincelestes* (BONAPARTE & ROUGIER, 1987), and in some living eutherians (elephants, some hyraxes, some rodents; MARSHALL, 1979). In some late Cretaceous eutherians from Asia (*Asioryctes*, *Kennalestes*, *Barunlestes*) the jugal is long, extends to the anterior edge of the glenoid fossa, but does not form a preglenoid process (KIELAN-JAWOROWSKA, 1981; 1984). The presence of a preglenoid process of the jugal is clearly a plesiomorphic state for metatherians, and the presence of this state in *Vincelestes* and some eutherians suggests that it is plesiomorphic for Theria as well. *Pucadelphys* thus retains the plesiomorphic metatherian (and therian) state.

Foramina of Skull

Pucadelphys retains two states which are regarded by some workers as plesiomorphic for Tribosphenida: V2 exits skull through foramen rotundum in alisphenoid (KERMACK *et al.*, 1981: 135), and presence of a foramen lacerum medium (MACINTYRE, 1967; ARCHER, 1976a). However, a foramen rotundum does not occur in *Kennalestes* or *Asioryctes*, and KIELAN-JAWOROWSKA (1981: 65) regarded a "foramen rotundum confluent with sphenorbital fissure" as the plesiomorphic therian state. The earliest known foramen rotundum in a eutherian occurs in the ?middle Campanian age *Barunlestes* (KIELAN-JAWOROWSKA & TROFIMOV, 1980).

Transverse canal. — There is no transverse canal in *Morganucodon* (KERMACK *et al.*, 1981), monotremes (WATSON, 1916), multituberculates (KIELAN-JAWOROWSKA *et al.*, 1986), Deltatheroida (KIELAN-JAWOROWSKA & NESSOV, 1990), Borhyaenoidea (except for a possible vestige in *Lycopsis*; MARSHALL, 1977: 415), *Pucadelphys*, some didelphids (i.e. *Caluromys*) and some dasyurids (some *Planigale*) (ARCHER, 1976a) or in late Cretaceous eutherians from Asia (*Asioryctes*, *Barunlestes*, *Kennalestes*, *Zalambdalestes*; KIELAN-JAWOROWSKA, 1981; 1984; KIELAN-JAWOROWSKA & TROFIMOV, 1980). Among metatherians a transverse canal occurs in thylacinids, myrmecobiids, peramelids, most didelphids and most dasyurids (ARCHER, 1976a).

ARCHER (1976a) regarded a transverse canal as a plesiomorphic state for metatherians, yet the distribution of this feature suggests that its absence was the plesiomorphic state for mammals. If this polarity is true, then a transverse canal evolved multiple times within metatherians, a

Source : MNHN, Paris

position supported by data in ARCHER (1976a: 307). For example, when present, the transerse canal, which transmits a major venous sinus that drains the base of the brain around the pituitary, varies considerably in size and morphology; "in dasyurids, thylacinids, some didelphids (e.g. *Marmosa* and *Monodelphis*) the canal passes not only into endocranium but also transversely through the basisphenoid", sometimes "via more than one canal". In these taxa the transverse venous sinus "may enter the endocranium via the sulci for the entocarotid canals", while in other taxa (e.g. peramelids and other didelphids) "both ends of this canal lead anteriorly for a considerable distance before communicating transversely through the basisphenoid".

ARCHER (1976a: 307) stressed that taxa which lack this canal have a venous drainage pattern considerably different from those taxa in which it is present. In some species of *Planigale*, for example, the "venous sinus passes transversely via the anterior edges of the enormous foramina pseudovale [*sic*, see below] which are so large that they incise the alisphenoid in the normal position of the transverse canal". Given the arrangement in some species of *Planigale*, we speculate that in metatherians like *Pucadelphys* which lack this canal, part of the venous drainage around the pituitary may leave the skull through the large foramen ovale. *Pucadelphys*, which lacks a transverse canal, retains the plesiomorphic metatherian (and mammalian) state.

Foramen ovale. — This term is used (*sensu* KIELAN-JAWOROWSKA *et al.*, 1986: 584) to designate the foramen which transmits the mandibular branch of the trigeminal nerve (V3). Within this definition is included the foramen "pseudovale" of earlier workers, a term which KIELAN-JAWOROWSKA *et al.* (1986: 584) "rejected as prejudicial to possible homology of anterior lamina of petrosal with part of mammalian alisphenoid (PRESLEY, 1981; KEMP, 1983)". This move took into consideration the fact that the shape of this foramen and detailed relations with surrounding bones vary within mammals, and that MACINTYRE's (1967) use of "pseudovale" is not consistent regarding these relationships since the foramen may either be totally surrounded by the anterior lamina or be in the junction between two or more bony elements. Because of this, "pseudovale" was regarded as not being a clear-cut alternative to ovale and its use implies a false impression of precision of definition (PRESLEY, personal communication, 1989). Thus, the term ovale is used in preference for homology regarding transmittal of the V3 and gives no weight to the bones surrounding the V3 in different mammal groups.

A great deal of confusion regarding the term ovale and "pseudovale"has resulted from the studies of MACINTYRE (1967) and ARCHER (1976a). MACINTYRE, for example, recognized a "pseudovale" in some living eutherians (i.e. some perissodactyls, artiodactyls, rodents) which formed as a result of the disappearance of a true foramen ovale (which was surrounded entirely by the alisphenoid) by its union with the foramen lacerum medium, which primitively in mammals is located at the junction of the alisphenoid-basisphenoid-basioccipital-petrosal (MACINTYRE, 1967: 834). In this sense, MACINTYRE's "pseudovale" is derived from an ancestral (plesiomorphic) state in which a true foramen ovale was surrounded by the alisphenoid which in turn is derived from yet another ancestral state in which a "pseudovale" was located between the anterior lamina of the petrosal and the alisphenoid. MACINTYRE's "pseudovale" is thus used in two significantly different non homologous contexts: true "pseudovale" (as in cynodonts, tritylodonts, monotremes) - true ovale (a derived state in generalized tribosphenids) - and "pseudovale" (=true ovale + foramen lacerum medium), (another derived state, in some living eutherians).

Source : MNHN, Paris

ARCHER (1976a) recognized a foramen ovale and "pseudovale" in the taxa he studied, and in some cases identified both on the same side of the same specimen (i.e. most Didelphidae: 307). He defined (p. 219) his "pseudovale" as: "Transmits cranial nerves. Sometimes carries very small arterial or venous anastomoses linking internal cranial and external cranial vessels and sometimes near its posterior edge, carries small branch of internal carotid artery into eustachian canal". In his Plate 1 where he labels this foramen on specimens, what he calls the "pseudovale" is in reality the medial lacerate foramen as evidenced by its position at the alisphenoid-basioccipital- basisphenoid-petrosal junction (MACINTYRE, 1967: 834). In other instances, ARCHER uses "pseudovale" *sensu* MACINTYRE (1967) in part, meaning the foramen formed by union of the medial lacerate foramen and ovale. ARCHER thus uses "pseudovale" in reference to two different nonhomologous foramina. However, ARCHER's use of foramen ovale appears to be correct (i.e. foramen in alisphenoid which transmits V3) and it is interesting that he regards (p. 307) its absence as a dasyurid plesiomorphy. Because ARCHER used the presence, absence and structural variation of his "pseudovale" and ovale in phylogenetic inference, his conclusions based on these features need reconsideration.

Subsquamosal foramen. — This foramen occurs in *Pucadelphys*, in all metatherian groups studied by ARCHER (1976a: 314) and in the late Cretaceous eutherians *Asioryctes* and *Kennalestes* (KIELAN-JAWOROWSKA,1981: 61). ARCHER (1976a) noted that this foramen is variably developed: in some specimens it occurs on one side of the skull but not the other, while in other specimens it lies adjacent to the postglenoid foramen and is separated from it by only a splint of bone. The presence of this foramen represents a plesiomorphic state within Theria (KIELAN-JAWOROWSKA, 1981: 65).

Postzygomatic foramen. — This foramen occurs in *Pucadelphys* and in all metatherian groups studied by ARCHER (1976a: 314). It is a plesiomorphic feature within Metatheria.

EAR REGION

Pucadelphys retains the following states which are plesiomorphic for Tribosphenida: a triossicular middle ear mechanism (MIAO & LILLEGRAVEN, 1986; KEMP, 1983); an inflated promontorium to house the spiral cochlea (MACINTYRE, 1972; PROTHERO, 1983: 1044); a fully coiled cochlea (380°) (MIAO & LILLEGRAVEN, 1986; WIBLE, 1990); a fossa incudis with prominent lateral wall formed by the squamosal (WIBLE, 1990); a true aqueductus cochleae (KERMACK *et al.*, 1981: 137; WIBLE, 1990); the internal acoustic meatus is a broad shallow pit with foramina which transmit a branch of the facial nerve (VII) and two branches of the acoustic nerve (VIII) (PROTHERO, 1983: 1041); the presence of a posttemporal foramen (WIBLE, 1990); and the presence of a lateral head vein (absence of this vein is a eutherian synapomorphy; MARSHALL, 1979; WIBLE, 1990). It also has three states which are metatherian synapomorphies: the prootic canal is reduced in length and width, and does not open endocranially (absence of this canal is a eutherian synapomorphy; WIBLE, 1990); the prootic sinus continues onto the squamosal side of the petromastoid within a deep sulcus (WIBLE, 1990); and the presence, on the squamosal side of the petromastoid, of a sphenoparietal emissary vein which occupies a deep sulcus continuous with the sulcus for the prootic sinus, and exits skull through the postglenoid foramen (WIBLE, 1990).

Source : MNHN, Paris

Ossified auditory bulla. — In *Pucadelphys* there is no evidence of an ossified auditory bulla. This same state occurs in monotremes, soricids, some talpids, and some fossil eutherians (i.e. *Asioryctes*, *Kennalestes*, *Palaeoryctes*) and apparently represents the plesiomorphic mammalian state (NOVACEK, 1977: 141). "A condition similar to that in the monotreme *Tachyglossus*, where the tympanic cavity was bordered ventrally by a thin connective tissue (dense fibrous and/or areolar) membrane located between the ventromedial surface of the nearly horizontal tympanic ring and the ventral surface of the petrosal, was the most primitive condition in monotremes, marsupials, and placentals" (NOVACEK, 1977: 144) (however, see below for discussion on the orientation of the typmanic ring).

Based on an authoritative study of fossil and living metatherians, ARCHER (1976a: 310) concluded that, among living taxa, didelphids were most plesiomorphic in aspects of their bullar morphology. REIG *et al.* (1987: 22) suggested that, among living didelphids, *Metachirus* and *Philander* were the most generalized. In these taxa the ossified bulla is incomplete: a small tympanic process of the alisphenoid occurs anteriorly, a small tympanic process of the pars petrosa of the petromastoid occurs posteriorly, and much of the middle ear in macerated skulls is open ventrally. This same architecture was regarded as the plesiomorphic metatherian bullar state by NOVACEK (1977) and apparently occurred in the late Cretaceous stagodontid *Didelphodon vorax* (CLEMENS, 1966: 55). There are thus two features (both absent in *Pucadelphys*) which warrant special consideration in the evolution of the metatherian bulla: the ossified tympanic process of the alisphenoid and the tympanic process of the pars petrosa.

An ossified tympanic process of the alisphenoid occurs in the vast major of metatherians and is generally regarded as a synapomorphy of that group (KIELAN-JAWOROWSKA & NESSOV, 1990), although its phylogenentic value has been recently questioned by MUIZON (1994). This feature is, however, absent in borhyaenoids [with the exception of *Cladosictis* and *Sipalocyon* (MUIZON, 1994)], in vombatids (PATTERSON, 1965), and in what appears to be a late Cretaceous metatherian that was figured but not discussed by MACINTYRE (1967, fig. 3). KIELAN-JAWOROWSKA (1981: 61) suggested that "the marsupial alisphenoid bulla originated from the enlarged quadrate ramus of the alisphenoid of early therians" and that in late Cretaceous eutherians (*Asioryctes* and probably *Kennalestes*) "a strongly inflated quadrate ramus of the alisphenoid occupies the same position as the alisphenoid bulla in marsupials and is probably homologous to it". However, in eutherians the alisphenoid rarely contributes to the formation of the ossified bulla and in those taxa where it is developed (i.e. macroscelidids, some insectivores; NOVACEK, 1977; SEGALL, 1970) it has a different shape and occurs in a different location than in metatherians (KIELAN-JAWOROWSKA, 1981: 61-62). Furthermore, in insectivores "the tympanic process of the basisphenoid takes the place of the tympanic process of the alisphenoid of marsupials" (SEGALL, 1970: 169). These observations clearly suggest that the ossified tympanic wing of the alisphenoid in metatherians and eutherians are nonhomologous and evolved independently in each group. This view is supported by the fact that an ossified alisphenoid bulla is absent in monotremes (WATSON, 1916), in the early Cretaceous eupantothere *Vincelestes* (BONAPARTE & ROUGIER, 1987; ROUGIER & BONAPARTE, 1988), in *Pucadelphys*, in *Mayulestes* (MUIZON, 1994) and in some late Cretaceous eutherians (KIELAN-JAWOROWSKA, 1981; 1984). Furthermore, MUIZON (1994) has shown that the absence of tympanic

Source : MNHN, Paris

process of the alisphenoid in *Mayulestes* and in most other borhyaenoids is a symplesiomorphy within the superfamily [not a reversal as stated by others (MARSHALL & KIELAN-JAWOROWSKA, 1992)] and that its presence in *Cladosictis* and *Sipalocyon* is a synapomorphy of this clade. The absence of a tympanic process of the alisphenoid in the didelphid *Pucadelphys* reinforces MUIZON's statement that this structure must have appeared several times during marsupial evolution and should not be used to diagnose this group of mammals.

The tympanic process of the pars petrosa (*sensu* REIG *et al.*, 1987; =rostral tympanic process of the petrosal, WIBLE, 1990; ectotympanic process of the periotic, ARCHER, 1976a: 230) is "intimately related" to the posteroventral end of the ossified ectotympanic; these bones are typically in contact but never fused (ARCHER, 1976a: 230). A tympanic process of the pars petrosa is absent and the promontorium is smooth in *Sinoconodon*, morganucodontids, triconodontids, *Vincelestes*, many metatherians (Deltatheroida, *Pucadelphys*, most Borhyaenoidea; living Phalangeridae, Vombatidae, and possibly Phascolarctidae), and many eutherians (late Cretaceous taxa from Asia, many Cenozoic and living goups) (WIBLE, 1990). A low ridge which may represent an incipient state of this structure occurs in the metatherian *Didelphodon vorax* and in Petrosal Types A-D of Wible (1990). This feature is well developed in living metatherians (except those mentioned above), in some eutherians (euprimates, erinaceomorphs), possibly in some multituberculates, and monotremes (although in this group it is not clearly homologous with that in metatherians and eutherians; WIBLE, 1990). The distribution of this structure among various groups thus suggests that mammals primitively had a smooth promontorium and lacked a tympanic process of the pars petrosa. WIBLE (1990) concluded that the absence of this feature was a plesiomorphic state for Eutheria, but was uncommital about the plesiomorphic state in Metatheria, suggesting only "that ridges and processes have been added to and lost from the promontorium a number of times in marsupials". We believe that metatherians (as in *Pucadelphys*) primitively lacked this structure and that it evolved independently in various lineages, possibly in association with the development and enlargement of an ossified auditory bulla.

Orientation of ectotympanic and tympanic membrane. — In living metatherians and eutherians (except soricids and some talpids) the ossified ectotympanic and tympanic membrane are oriented in a nearly vertical plane, and this state has been regarded as a therian synapomorphy (KEMP, 1983: 375). However, this view is not corroborated by fossil or ontogenetic evidence which suggests two other possibilities. First, NOVACEK (1977) suggested that the ectotympanic was primitively subhorizontal in position. This possibility is supported by the horizontal position of the ectotympanic in the living monotreme *Tachyglossus* (NOVACEK, 1977: 144, Fig. 6), in the late Paleocene multituberculate *Lambdopsalis* (MIAO & LILLEGRAVEN, 1986), and the knowledge that the ectotympanic is oriented horizontally in the early ontogeny in all mammals and remains in this position in monotremes but rotates to an inclined position in most therians (DE BEER, 1937) which thus represents a derived state (ROWE, 1988). Second, KIELAN-JAWOROWSKA (1981) suggested that the ectotympanic was primitively inclined at an angle of 45° from horizontal. This possibility is based on the observations that in cynodonts and some early mammals with a double jaw joint (i.e. *Morganucodon*) the angular (=ectotympanic) is sharply inclined (KIELAN-JAWOROWSKA, 1981: 38). Support for this possibility came with the discovery of the late Cretaceous eutherians

Source : MNHN, Paris

Asioryctes and *Kennalestes* in which the *in situ* ectotympanic was released from the lower jaw but still retains its primitive anterior position opposite the posterior part of the dentary and is roughly parallel to it at 45° from horizontal. If this does indeed represent the primitive therian state, then both the subhorizontal state in *Tachyglossus* and the near vertical state in some living metatherians and eutherians are derived conditions.

Yet, the same data base has been interpreted by some workers to support both possibilities (i.e. subhorizontal is primitive and inclined at 45° is primitive), suggesting that differences between the two are relative and in part semantic. The best example is NOVACEK's (1977: 145) paper in which he argues that "the last common ancestor of marsupials and placentals... and the most primitive members of each group... had a simple tympanic ring only slightly inclined to the horizontal plane of the skull" which resembled the monotreme-like state. In his fig. 7a he illustrates this plesiomorphic state with the ectotympanic inclined at 35° from horizontal, while on p. 141 he notes that "the simple ring-shaped ectotympanic lies at a low angle (less than 50°) to the horizontal plane of the skull", a state seen in monotremes, soricids, some talpids, and possibly in *Asioryctes* and *Palaeoryctes*.

In *Pucadelphys* there is no evidence of an ossified ectotympanic, nor are there facts to demonstrate that one was present. Its absence is attributed to destruction during fossilization. The tympanic membrane was apparently subvertical or slightly obliquely oriented at an angle much larger than 45° from horizontal, because this is the general orientation of the fenestra vestibuli (see YPFB Pal 6110) and the ectotympanic parallels it in Recent mammals (J. WIBLE, written communication, 1990). Therefore, whatever the primitive condition is (either sub horizontal or at 45°) the inferred subvertical position of the ectotympanic of *Pucadelphys* would represent a derived condition.

Auditory sinuses. — "Auditory sinuses... are cavities within or between bones in the auditory region of the skull (other than the epitympanic recess) which communicate directly with the epitympanic recess" (ARCHER, 1976a: 226). Such sinuses are absent in *Morganucodon* (KERMACK *et al.*, 1981), monotremes (WATSON, 1916), *Vincelestes* (BONAPARTE & ROUGIER, 1987), late Cretaceous eutherians (*Asioryctes*, *Barunlestes*, *Kennalestes*, *Zalambdalestes*; KIELAN-JAWOROWSKA, 1981; 1984; KIELAN-JAWOROWSKA & TROFIMOV, 1980), and generalized living eutherians (VAN KAMPEN, 1905; NOVACEK, 1977). Among Cenozoic and living metatherians, auditory sinuses are primitively absent, although a small alisphenoid hypotympanic sinus appears in all groups studied by ARCHER (1976a) except some borhyaenoids. The absence of auditory sinuses in *Pucadelphys* thus represents the plesiomorphic state for mammals.

Pars mastoidea contribution to occiput. — The pars mastoidea has an extensive exposure on the occiput in monotremes (*Tachyglossus*), in late Cretaceous eutherians (*Asioryctes*, *Kennalestes*; KIELAN-JAWOROWSKA, 1981, fig. 2), and among metatherians in *Didelphodon vorax*, *Eodelphis browni*, Petrosal Types A and B from the late Cretaceous (WIBLE, 1990), in *Mayulestes* (MUIZON, 1994) and in many taxa studied by ARCHER (1976a). An extensive contribution of the pars mastoidea to the occiput also occurs in *Pucadelphys*, and this apparently represents the plesiomorphic state for Tribosphenida.

Source : MNHN, Paris

Mastoid and paroccipital processes. — These processes are either absent or only incipiently developed in *Morganucodon*, monotremes, *Vincelestes* (BONAPARTE & ROUGIER, 1987), in late Cretaceous Asiatic eutherians (*Asioryctes*, *Barunlestes*, *Kennalestes*, *Zalambdalestes*; KIELAN-JAWOROWSKA, 1981; 1984; KIELAN-JAWOROWSKA & TROFIMOV, 1980), and in most generalized metatherians (*Mayulestes*; Myrmecobiidae; most Dasyuridae; Caenolestidae; Microbiotheriidae; some Didelphidae, *Lestodelphys*, *Monodelphys*) (ARCHER, 1976a; REIG *et al.*, 1987). A well developed mastoid and/or paroccipital process does occur in various late Cretaceous (WIBLE, 1990), Cenozoic and Recent metatherian groups (ARCHER, 1976a; REIG *et al.*, 1987), where they are derived and apparently evolved independently in various lineages (ARCHER, 1976a). The absence of a paroccipital process and small size of mastoid process as occur in *Pucadelphys*, apparently represent or approximate the plesiomorphic state for mammals.

Shape of fenestra vestibuli and stapedial footplate. — The ratio of length to width of the fenestra vestibuli approximates or represents that of the stapedial footplate. In the monotreme *Tachyglossus* this ratio is 1.0 (SEGALL, 1970: 203, fig. 26); in *Morganucodon* 1.1, triconodontids and Bug Creek multituberculates 1.3, *Vincelestes* 1.0 (WIBLE, 1990); and the late Paleocene multituberculate *Lambdopsalis* bulla 1.0 (MIAO & LILLEGRAVEN, 1986). Among metatherians, living Didelphidae have ratios ranging from 1.3 - 1.5 (SEGALL, 1970), *Didelphodon vorax* 1.4 (ARCHIBALD, 1979), late Cretaceous taxa studied by WIBLE (1990) range from 1.3 - 1.6, while living *Dromiciops* and *Macropus* have 2.1 (SEGALL, 1970). Bug Creek eutherians range from 2.0 - 2.4 (ARCHIBALD, 1979) and living eutherians 1.8 - 2.9 (SEGALL, 1970). These data suggest that: a circular fenestra vestibuli with a ratio of 1.0 is plesiomorphic for Mammalia (ARCHIBALD, 1979; SEGALL, 1970; PROTHERO, 1983; MIAO & LILLEGRAVEN, 1986; WIBLE, 1990); a slightly ovoid fenestra with a ratio of 1.3 is a synapomorphy of metatherians and possibly Tribosphenida; *Pucadelphys* with a ratio of 1.4 approximates the plesiomorphic state for metatherians; and an elliptical fenestra with a ratio of 1.8 is a synapomorphy of eutherians (WIBLE, 1990).

Stapedial artery. — The stapedial artery, a branch of the internal carotid artery, occurs in embryos of living monotremes, metatherians and eutherians, but only in adults of *Ornithorhynchus* and some eutherians (PRESLEY, 1979). As evidenced by a groove which marks the course of this artery on the pars petrosa of monotremes and some eutherians, it is believed to have been present in multituberculates (KIELAN-JAWOROWSKA *et al.*, 1986), late Cretaceous eutherians from Asia (*Barunlestes*, *Zalambdalestes*; KIELAN-JAWOROWSKA, 1984: 108) and North America (WIBLE, 1990) and various Cenozoic eutherians (PRESLEY, 1979). In metatherians, a stapedial artery is absent in adults of all living taxa (TANDLER, 1899; PRESLEY, 1979) and the groove is absent in fossil taxa (ARCHER, 1976a; ARCHIBALD, 1979; CLEMENS, 1966; WIBLE, 1990). The presence of a stapedial artery in adults is thus a plesiomorphic state for mammals (PRESLEY, 1979: 241, fig. 3), while the absence of this artery in adult metatherians represents a synapomorphy of that group (WIBLE, 1990). *Pucadelphys*, which lacks a groove for this artery, has the plesiomorphic state for metatherians.

Course of internal carotid artery. — The course of the internal carotid artery, which is derived from the embryonic dorsal aorta, has two basic states in mammals which "arise by a process of differential growth affecting the relative positions of the dorsal aorta and cochlear promontory" (PRESLEY, 1979: 238). WIBLE (1986) cautions that the position of the internal carotid

Source : MNHN, Paris

artery with regard to the cochlear promontory cannot be inferred from the location of the entocarotid foramen alone. The probable plesiomorphic state for mammals (ARCHIBALD, 1979; PRESLEY, 1979) is called the medial internal carotid artery (MICA) where the vessel passes medial to the cochlear promontory on its way to the entocarotid foramen and leaves little or no trace on the bone. This state occurs in monotremes, all metatherians (MACINTYRE, 1972: 291), in late Cretaceous Asian eutherians (KIELAN-JAWOROWSKA, 1981: 58-59; 1984: 115; KIELAN-JAWOROWSKA & TROFIMOV, 1980), and in some living eutherians [e.g. rodents, rabbits, ungulates (PRESLEY, 1979; KIELAN-JAWOROWSKA, 1981: 57)]. The apomorphic state is called the promontory internal carotid artery (PICA) where the vessel passes upon or lateral to the cochlear promontory, often in a sulcus. This state occurs in some primates, insectivores and some carnivorans, and may have evolved multiple times (PRESLEY, 1979). *Pucadelphys* thus retains the plesiomorphic MICA state, where the course of the internal carotid is marked by a shallow sulcus.

In addition, the presence of a large entocarotid foramen between the alisphenoid and basisphenoid which transmits the internal carotid as in *Pucadelphys* appears to be the plesiomorphic state in metatherians (ARCHER, 1976a), eutherians (KIELAN-JAWOROWSKA, 1981), and their tribosphenid ancestor.

Sulcus for facial nerve. — A sulcus for the facial nerve on the petromastoid has been regarded as a synapomorphy of metatherians and eutherians (i.e. MACINTYRE, 1972); yet, this feature also occurs in morganucodontids, triconodontids, multituberculates, monotremes and the eupantothere *Vincelestes*; it is therefore a plesiomorphy for mammals (WIBLE, 1990). *Pucadelphys* retains the plesiomorphic state.

Inferior petrosal sinus and foramen. — The inferior petrosal sinus joins posteriorly with the internal jugular vein and exits the skull through the inferior petrosal (=internal jugular) foramen (ARCHIBALD, 1979). The term internal jugular foramen (=canal) was proposed by ARCHER (1976a) to replace the posterior carotid foramen of GREGORY (1910: 233) and PATTERSON (1965: 2) which they erroneously believed transmitted a branch of the internal carotid artery; this error was perpetuated by CLEMENS (1966: 73) and MARSHALL (1977, 1978).

A sulcus for the inferior petrosal sinus occurs in *Morganucodon*, monotremes, and in many metatherians and eutherians, and apparently represents a plesiomorphy (*nec* therian synapomorphy of MACINTYRE, 1972) within mammals. An inferior petrosal foramen occurs nearly universally in metatherians (ARCHER, 1976a: 309) but is apparently absent in some (microbiotheres, *Acrobates*, possibly *Phascolarctos*; PATTERSON, 1965: 6), and is widely distributed among fossil and living eutherians (PATTERSON, 1965). Its presence apparently represents the plesiomorphic state for Tribosphenida. *Pucadelphys* retains both an inferior petrosal sinus and foramen.

Anterior lamina. — The anterior lamina is a bony blade located at the anterodorsal border of the petrosal in several primitive mammals: *Adelobasileus*, *Haldanodon*, *Megazostrodon*, *Morganucodon*, *Sinoconodon*, *Trioracodon*, multituberculates, *Vincelestes*, and monotremes (see WIBLE & HOPSON, 1993 for original references). The anterior lamina is perforated by a foramen (foramen ovale) for the V3 (mandibular branch of the trigeminal nerve), in *Morganucodon*, *Sinoconodon*, *Adelobasileus*, most multituberculates, *Vincelestes*, and *Ornithorhynchus*. However, there is a single trigeminal foramen between the anterior lamina and alisphenoid in *Megazostrodon*

Source : MNHN, Paris

and *Haldanodon* (WIBLE & HOPSON, 1993). The V2 (maxillary branch of the trigeminal nerve) is also enclosed in the anterior lamina in *Morganucodon*, *Sinoconodon*, *Adelobasileus*, and *Vincelestes*.

In the non-tribosphenic taxa mentioned above "the anterior lamina contributes to the lateral wall of the cavum epiptericum, the extradural space within which the trigeminal ganglion lies" (WIBLE & HOPSON, 1993: 47). KERMACK *et al.* (1981: 119), in their authoritative study of the skull anatomy of *Morganucodon*, state that the trigeminal ganglion (= semilunar ganglion) lies in a deep pocket of the medial side of the anterior lamina, lateral to the medial opening of the aqueductus Fallopii for the facial (VII) cranial nerve. A similar condition is observed in *Trioracodon* (KERMACK, 1963: 87), in multituberculates (KIELAN-JAWOROWSKA *et al.*, 1986), in *Haldanodon* (LILLEGRAVEN & KRUSAT, 1991: 97) and in *Ornithorhynchus* (ZELLER, 1989a, b). The medial aspect of the anterior lamina of *Vincelestes* has not been described. In the recent didelphid *Monodelphis domestica*, the trigeminal ganglion lies anterolateral to the hiatus Fallopii in a shallow fossa of the alisphenoid and the anterior border of the petrosal (MAIER, 1987; HOPSON & ROUGIER, 1993). In *Pucadelphys*, the fossa observed on the medial side of the lamina of the pars petrosa anterolateral to the hiatus Fallopii, is interpreted here as the Gasserian fossa or fossa for the trigeminal ganglion. Since this ganglion is located in the anterior lamina of the petrosal in *Morganucodon*, *Trioracodon*, *Haldanodon*, multituberculates, and *Ornithorhynchus*, the anterior wing of the pars petrosa of *Pucadelphys* is interpreted here as a structure homologous to the anterior lamina of these early mammals. Furthermore, the anterior lamina of *Pucadelphys* occupies the same position as the anterior lamina in early cynodonts (KEMP, 1983: 375), morganucodonts (KERMACK *et al.*, 1981), triconodonts (KERMACK, 1963; CROMPTON & JENKINS, 1979, fig. 3-5 A-C), and *Vincelestes* (HOPSON & ROUGIER, 1993). The anterior lamina of *Pucadelphys* is greatly reduced when compared to that of *Morganucodon*, *Sinoconodon*, multituberculates and *Vincelestes* but it is larger than in any other marsupials. However, this feature does not constitute a true novelty for the group since WIBLE (1990: 200) and WIBLE & HOPSON (1993: 60), stated that the great reduction or absence of the anterior lamina of the petrosal is a synapomorphy of the marsupials and eutherians, therefore implicitly accepting the presence of a reduced anterior lamina in some Tribosphenida.

The presence of an anterior lamina in *Pucadelphys* confirms WIBLE's assertion that "the anterior lamina...may not be entirely absent in marsupials" (WIBLE, 1990: 200). As explained by this author, "the prootic canal runs through the anterior lamina of the petrosal in *Sinoconodon*, morganucodontids, triconodontids, multituberculates, and *Vincelestes*". The occurrence of a prootic canal in some marsupials seems to confirm that the structure it passes through may represent a reduced anterior lamina (in peramelids, dasyurids and some didelphids). However, WIBLE & HOPSON (1994) have recently shown that the prootic canal of marsupials is probably not homologous to that in morganucodonts, triconodonts, multituberculates, and *Vincelestes*. If they are correct, therefore, the prootic canal should not be used for homologies of the anterior lamina.

The anterior lamina of *Pucadelphys* differs from that of the non-tribosphenic mammals mentioned above, because it does not participate in the closure of the lateral wall of the skull; it is covered laterally by the squamosal and the alisphenoid which articulate together and replace the

Source : MNHN, Paris

anterior lamina in that function. At the level of the anterior lamina of *Pucadelphys,* the lateral wall of the skull is thus duplicated; it is formed by the alisphenoid and the squamosal laterally and by the petrosal (anterior lamina) medially. This condition demonstrates that the anterior lamina was expelled from the lateral wall of the skull before it totally regressed. As a consequence of the reduction of the anterior lamina, in marsupials, the mandibular branch of the trigeminal nerve (V3) exits the skull (via the foramen ovale) between the alisphenoid and the anterior border of the petrosal (this condition is very clear in the early diverging borhyaenoid marsupial *Mayulestes*). In *Pucadelphys*, however, the anterolateral border of the petrosal (the posterior edge of the foramen ovale) probably retains part of the anterior lamina; therefore, the foramen ovale of *Pucadelphys* is located between the alisphenoid and the anterior lamina of the petrosal. In eutherians the foramen ovale is located in the alisphenoid.

In morganucodonts, triconodonts, *Sinoconodon* and *Adelobasileus* the anterior lamina is large and the alisphenoid is relatively short anteroposteriorly but tall dorsoventrally (KERMACK, 1963; and KERMACK *et al.*, 1981; LUCAS & LUO, 1993; CROMPTON & LUO, 1993). Monotremes have a large anterior lamina posterodorsal to a reduced (anteroposteriorly and dorsoventrally) alisphenoid and posteroventral to the orbitosphenoid. In most multituberculates the anterior lamina is large, posterodorsal (or posterior) to a large orbitosphenoid and posterodorsal to the alisphenoid (KIELAN-JAWOROWSKA, 1971; 1974; KEMP, 1988). The alisphenoid of multituberculates is generally small (KIELAN-JAWOROWSKA, 1971; KEMP, 1982), but in the multituberculate *Lambdopsalis* it is large, totally separates the anterior lamina from the orbitosphenoid, and has tribosphenid proportions (MIAO, 1988). Large anterior lamina and alisphenoid also occur in *Vincelestes* (ROUGIER & BONAPARTE, 1988; HOPSON & ROUGIER, 1993).

The homologies of the anterior lamina and alisphenoid in monotremes and in the other non-tribosphenic mammals mentioned above have been discussed by PRESLEY & STEEL (1976), PRESLEY (1980; 1981), and HOPSON & ROUGIER (1993). The status of the anterior lamina of monotremes has been abundantly studied in order to elucidate whether or not it is homologous to the anterior lamina of the other non-tribosphenic taxa mentioned above. The anterior lamina in living monotremes is an intramembranous ossification called the "lamina obturans" which fuses secondarily to the pars petrosa (VANDEBROEK, 1964; WIBLE, 1990). PRESLEY (1981) has confirmed that the "lamina obturans", in living monotremes, is an independent center of intramembranous ossification within the sphenobturator membrane. This author also states that "there seem to be no fundamental difference between therians and monotremes in the early development of this bone. Difference arise only when it fuses with its neighbours. ... Cynodonts may have had an anterior part contributing to the broad blade of the epipterygoid and a posterior forming the smaller anterior process of the petrosal". The proportions of these two parts of the lamina obturans may have varied since in triconodonts (KERMACK, 1964) and morganucodonts (KERMACK *et al.*, 1981) the anterior lamina of the petrosal is large and the epipterygoid blade small. In multituberculates, given the extreme reduction of the alisphenoid (epipterygoid) the lamina obturans may have contributed extensively to the petrosal, approaching the monotreme condition (PRESLEY, 1981). These studies suggest that the anterior lamina fused to the pars petrosa as in early cynodonts, morganucodonts and triconodonts is derived from the posterior part of the "lamina obturans",

Source : MNHN, Paris

which apparently was an ossification independent from the pars petrosa; while the anterior lamina in monotremes, multituberculates represents some combination of posterior and anterior part of the "lamina obturans". MIAO (1988) has suggested that the "lamina obturans" has an apparent plasticity for alliance within itself and with adjacent bones, and this could explain the within group variability of the anterior lamina in multituberculates. Considering that the blade of the alisphenoid and the anterior lamina of the petrosal are probably equivalent, PRESLEY (1981) concluded that a simple change in the fusion of these elements during development could produce a therian pattern of the lateral wall of the braincase. This was ratified by KEMP (1983: 374), who noted: "the sidewall of the non-therian braincase is apparently homologous [s.l.] with the sidewall of the modern therian braincase, and the two groups differ only in the relatively trivial matter of which bone the anterior lamina [s.l.] finally fuses with towards the end of ontogeny".

Recently, HOPSON & ROUGIER (1993) have questioned the interpretation of PRESLEY & STEEL (1976), PRESLEY (1981), and KEMP (1983). PRESLEY (1981) and ZELLER (1989 a, b) have demonstrated that in *Ornithorhynchus* the lamina obturans (anterior lamina) ossifies within the spheno-obturator membrane, entirely separate from the otic capsule and only in later development becomes synostosed to it (HOPSON & ROUGIER, 1993: 278). The lamina obturans of *Ornithorhynchus* begins to ossify in the dorsal part of the spheno-obturator membrane, quite distant from the ala temporalis (the endochondral portion of the alisphenoid) and only late in ontogeny it expands anteroventrally to contact the small alisphenoid (HOPSON & ROUGIER, 1993: 282). MAIER (1987) described the development of the alisphenoid of *Monodelphis domestica*. He demonstrated that the intramembranous portion of this bone is initiated adjacent to the ala temporalis and only at a fairly late ontogenetic stage expands posteriorly to contact the otic capsule. HOPSON & ROUGIER (1993: 283-284) therefore conclude that: "even though both elements form in the spheno-obturator membrane, the developmental evidence indicates that they are distinct, therefore non-homologous, ossifications". The monotreme lamina obturans is presumably homologous with the anterior lamina (HOPSON & ROUGIER, 1993: 284) and therefore, contrary to PRESLEY & STEEL (1976) and PRESLEY (1981), the anterior lamina is not homologous with the intramembranous portion (formed within the spheno-obturator membrane) of the alisphenoid. Furthermore, the alisphenoid of *Vincelestes* is similar to that of modern therians in its great anteroposterior expansion and its position relative to the otic capsule. It is noteworthy that in *Ornithorhynchus* the trigeminal ganglion lies in a fossa of the medial side of the lamina obturans (ZELLER, 1989b). Therefore, the homology of the monotreme lamina obturans with the anterior lamina (which we accept here) reinforces the interpretation of the anterior lamina of *Pucadelphys,* since the trigeminal ganglion appears to lie constantly in the same structure, the small fossa on the medial side of the anterior lamina lateral to the hiatus Fallopii.

The occurrence of a reduced anterior lamina in a marsupial is by no mean a surprise since the evolution of the therian (*Vincelestes* + marsupials + placentals) lateral wall of the braincase is characterized by the development of an anteroposteriorly elongated alisphenoid (observed in all therians) and the reduction and loss of the anterior lamina of the petrosal in the Tribosphenida. The presence, in *Pucadelphys*, of an anterior lamina, large for a marsupial but reduced when compared to that of *Vincelestes* (the sister group of the Tribosphenida), demonstrates that the

Source : MNHN, Paris

morphology of the lateral wall of the braincase of *Pucadelphys* is intermediate between that of *Vincelestes* and that observed in the other marsupials. Therefore, it may approximate the condition of the ancestral Tribosphenida. The morphology of the lateral wall of the braincase of *Pucadelphys* corroborates WIBLE (1990) and WIBLE & HOPSON (1993) synapomorphy of the Tribosphenida (marsupials + placentals): reduction or absence (interpreted here as loss) of the anterior lamina of the petrosal. It is also in agreement with the interpretation of *Vincelestes* as the sister group of marsupials + placentals (Tribosphenida) (ROW, 1993; and WIBLE & HOPSON, 1993). Furthermore, it corroborates the interpretation of HOPSON & ROUGIER (1993) who have refuted the hypotheses of PRESLEY & STEEL (1976) and PRESLEY (1981) on the homologies of the elements of the lateral wall of the mammalian braincase.

CONCLUSIONS

The skull of *Pucadelphys* represents a classic example of mosaic evolution. It has a commonly observed combination of plesiomorphic and apomorphic states which, collectively, complicates its placement in recent phylogenies (i.e. MARSHALL *et al.*, 1989; MARSHALL & KIELAN-JAWOROWSKA, 1992) although recent discoveries have shed some light to its interpretation (MUIZON, 1994). However that may be, it illustrates that we still have much to learn about early metatherian and tribosphenid evolution.

The vast majority of structures in the skull and dentary of *Pucadelphys* represents plesiomorphic states for Tribosphenida and/or Mammalia. A few features represent metatherian synapomorphies (i.e. cheek tooth formula P3/3 and M4/4; prootic canal reduced in length and width, and does not open endocranially; prootic sinus continues onto squamosal side of petromastoid within a deep sulcus; presence of sphenoparietal emissary vein which occupies a deep sulcus on squamosal side of petromastoid, is continuous with sulcus for prootic sinus, and exits skull through postglenoid foramen; length/width ratio of fenestra vestibuli; absence of stapedial artery) which securely demonstrate that *Pucadelphys* is a member of this group, as presently defined.

The remaining structures suggest contradictory affinities within Metatheria. The derived molar features agree perfectly with members of the Didelphidae (*sensu* MARSHALL *et al.*, 1989) and for this reason *Pucadelphys* has been assigned to this family (MARSHALL & MUIZON, 1988). However, *Pucadelphys* retains the plesiomorphic state of a non-staggered i3, while all other metatherians (except Microbiotheriidae) have the derived state of a staggered i3. It is also plesiomorphic in having I1-5 conical, equally spaced and I1 not hypsodont, while most other metatherians are derived in either having spatulate I1-5 (a synapomorphy of Australidelphia; MARSHALL *et al.*, 1989) or I1 hypsodont and separated from I2 (many Didelphidae and Dasyuridae).

The plesiomorphic mammal state of a clear nasal-lacrimal contact occurs among metatherians only in Borhyaenoidea, Deltatheroida (if they actually are metatherians) and the Australian *Wynyardia*, while all other known taxa (including *Pucadelphys*) have the derived state of a frontal-maxilla contact.

Source : MNHN, Paris

Pucadelphys lacks an ossified alisphenoid bulla, a feature present and traditionally regarded as a synapomorphy (KIELAN-JAWOROWSKA & NESSOV, 1990) in all other metatherians. The Deltatheroida, which apparently possess a tympanic process of the alisphenoid, are classified by KIELAN-JAWOROWSKA & NESSOV (1990) within the metatherians. The absence of a tympanic process of the alisphenoid in some Borhyaenoidea has been interpreted as representing a derived state from an ancestor which had an alisphenoid bulla (ARCHER, 1976a; MARSHALL & KIELAN-JAWOROWSKA, 1992). However, the morphology of the skull of *Mayulestes ferox*, a borhyaenoid from the early Paleocene of Tiupampa indicates that the lack of a tympanic process of the alisphenoid is the plesiomorph condition for the borhyaenoids (MUIZON, 1994). Furthermore, the absence of a tympanic process of the alisphenoid in *Pucadelphys*, an early Paleocene didelphoid may indicate its independent acquisition in the other members of the superfamily. It is noteworthy that a tympanic process is probably present in the late Cretaceous stagodontid, *Didelphodon* (CLEMENS, 1966) and in a probable marsupial (Asiadelphia) from the Barun Goyot Formation (middle Campanian) of Mongolia (TROFIMOV & SZALAY, 1993). This reinforces the idea that the tympanic process of the alisphenoid appeared several times independently within marsupials (MUIZON, 1994) and should not be used to diagnose this group, which, therefore, partially questions the inclusion of the Deltatheroida within the Metatheria (KIELAN-JAWOROWSKA & NESSOV, 1990).

The presence of an anterior lamina fused to the petromastoid, and a foramen ovale (exit of V3) which opens between the anterior lamina and alisphenoid represent the most peculiar structures in the skull of *Pucadelphys*. These features have not been reported as such in other tribosphenids, although their presence has been predicted in the tribosphenid ancestor because these states occur in non-tribosphenid mammals. Comparisons of *Pucadelphys* with *Vincelestes* (the sister group of the Tribosphenida) and with the other marsupials indicates that it represents a morphological stage of the structure of the lateral wall of the braincase, intermediate between the primitive (*Vincelestes*) and modern (tribosphenid) therians and therefore allows a better understanding of character states and evolution. It is probable that *Pucadelphys* represents or approximates the plesiomorphic state in the morphology of the lateral wall of the braincase of early Tribosphenida.

Pucadelphys thus appears to represent the paleontological confirmation of the hypothesis of HOPSON & ROUGIER (1994) who have refuted that of PRESLEY & STEEL (1976) and PRESLEY (1981) for the evolution of the tribosphenid ear region. If the skull of *Pucadelphys* was of early-late Cretaceous age and had a generalized tribosphenid molar structure, then it would probably be celebrated as the long sought "missing-link" and be readily accommodated and accepted into the current scheme of early tribosphenid evolution. However, *Pucadelphys* is a metatherian, has a derived didelphid molar structure, and is early Paleocene in age. Thus the predicted anterior lamina and foramen ovale bordered by it and the alisphenoid occur in a dentally derived and geologically recent metatherian.

Considering the major differences existing between *Pucadelphys* and the other didelphids (especially concerning the ear region and the lateral wall of the braincase), one could be tempted to classify it in a new family. However, as mentioned above, all the cranial features of *Pucadelphys* are plesiomorphic for marsupials and the only clearly derived features within marsupials concern

Source : MNHN, Paris

the dental morphology and relate *Pucadelphys* to the Didelphidae. We regard *Pucadelphys* as a primitive Didelphidae, member of the order Didelphimorphia (*sensu* MARSHALL *et al.*, 1989) because its molar structure (which is currently the foundation of metatherian systematics) is indistinguishable from that family. We thus give preference to molar structure in classifying *Pucadelphys* within Metatheria.

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Source : MNHN, Paris

TABLE 1.— Measurements (mm) of cheek teeth of *Pucadelphys andinus*.
Abbreviations: **CV**, coefficient of variation; **N**, number of specimen; **OR**, observed range of variation; **SD**, standard deviation; $\overline{X}$, mean.
TABLEAU 1.— Mesures (mm) des dents jugales de Pucadelphys andinus.
*Abréviations : **CV**, coefficient de variation ; **N**, nombre des spécimens ; **OR**, valeurs extrêmes observées ; **SD**, écart-type ; $\overline{X}$, moyenne.*

	P1		P2		P3		M1		M2		M3		M4		M1-3 / M1-4	P1-M3 / P1-M4
	L	W	L	W	L	W	L	W	L	W	L	W	L	W	L	L
Upper Cheek Teeth																
N	8	8	6	6	7	7	8	8	12	12	12	12	10	10	13	10
OR	0.8-1.0	0.4-0.6	1.5-1.6	0.8-0.9	1.6-1.9	0.8-1.0	1.7-2.0	1.8-2.0	1.7-2.1	2.2-2.4	1.7-2.0	2.3-2.6	1.0-1.2	2.2-2.3	4.8-5.4	8.5-9.3
$\overline{X}$	0.90	0.49	1.53	0.85	1.77	0.94	1.86	1.89	1.92	2.29	1.86	2.44	1.08	2.28	5.08	8.88
SD	0.07	0.06	0.05	0.05	0.10	0.07	0.10	0.08	0.09	0.09	0.09	0.10	0.09	0.04	0.16	0.28
CV	7.78	12.24	3.27	5.88	5.65	7.45	5.38	4.23	4.69	3.93	4.84	4.10	8.33	1.75	3.15	3.15
Lower Cheek Teeth																
N	7	7	9	9	9	9	11	11	9	9	10	10	9	9	10	7
OR	0.8-1.0	0.4-0.6	1.3-1.5	0.7-0.9	1.3-1.6	0.7-0.9	1.7-1.9	1.0-1.2	1.8-2.0	1.2-1.3	1.8-2.0	1.2-1.4	1.7-2.0	1.0-1.2	6.8-7.7	11.0-12.1
$\overline{X}$	0.87	0.51	1.42	0.77	1.47	0.80	1.80	1.09	1.89	1.24	1.90	1.28	1.83	1.13	7.07	11.30
SD	0.07	0.06	0.08	0.07	0.09	0.05	0.07	0.08	0.09	0.05	0.07	0.07	0.08	0.08	0.25	0.25
CV	8.05	11.76	5.63	9.09	6.12	6.25	3.89	7.34	4.76	4.03	4.21	5.47	4.37	7.08	3.54	3.10

Source : MNHN, Paris

Part III: Postcranial skeleton

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ABSTRACT

The earliest and most complete articulated skeletons of fossil metatherians yet known are represented by four specimens of *Pucadelphys andinus* from the Santa Lucía Formation (early Paleocene) at Tiupampa in southcentral Bolivia. Two sets of what are interpreted to be male-female pairs were found in a three dimensional, life-like, snout-rump position in burrow-nests that were apparently dug in a bank along a meandering river. The animals probablydie d as the result of a flood which entrapped them in their burrows and filled the latter with water and sediment. A detailed comparative study of the postcranial bones reveals that the vast majority of character states in *Pucadelphys* are regarded as mammalian, tribosphenic or metatherian plesiomorphies (e.g. atlas not perforated by transverse canal and with a persisting suture between the ossified intercentrum and atlantal arch; absence of transverse canal on axis, with possible unfused rib; absence of enclosed transverse canal on CV7; robust fibula; presence of ossified os marsupium; etc.). Character states of uncertain polarity include the presence of only one vertebra articulating with the ilium (fulcral vertebra), and a long non-prehensile tail. The tarsus has a bicontact upper ankle joint (UAJ) as in living Didelphidae; moreover the calcaneum shows a partially plantar orientation of the cuboid facet which can be interpreted as foreshadowing the specialisation of later Didelphidae; the situation then is more advanced than in the "plesiomorphic metatherian morphotype" of SZALAY (1982 a, b; 1984); the only characters of the latter persisting in *Pucadelphys* are the large peroneal process and the "remarkably broad transverse dimensions from peroneal process to the medial margin of the sustentaculum". Collectively these characters support the view, based on the study of the skull and dentition (MARSHALL & MUIZON, 1995), that *Pucadelphys* represents the plesiomorphic taxon within the family Didelphidae. Functional considerations of the skeletons suggest that *Pucadelphys* was essentially terrestrial, quite agile, and possessed limited bounding and digging capabilities.

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Source : MNHN, Paris

RÉSUMÉ

Troisième partie : le squelette postcrânien

Les squelettes les plus anciens et les plus complets de métathériens fossiles connus à ce jour sont représentés par quatre specimens de *Pucadelphys andinus*, en provenance de la Formation Santa Lucia (Paléocène inférieur), à Tiupampa, dans le sud de la Bolivie centrale. Deux ensembles de ce que nous avons interprété comme des couples mâle-femelle ont été conservés en trois dimensions, en position de vie, et disposés tête-bêche dans ce qui semble avoir été la berge d'un méandre fluviatile. Ces animaux sont apparemment morts à la suite d'une inondation qui les a piégés dans leur terrier en remplissant ce dernier d'eau et de boue. L'étude détaillée et comparée des os postcrâniens a révélé que la grande majorité des caractères de *Pucadelphys* peuvent être considérés comme étant dans un état plésiomorphe pour les Mammifères, les Tribosphenida et/ou les Métathériens (*e.g.* atlas imperforé et gardant une suture entre l'intercentre ossifié et l'arche atlantale ; axis dépourvu de canal transverse, mais possédant une côte libre persistante ; absence de véritable canal transverse sur CV7 ; fibula robuste ; présence d'un os marsupium ossifié ; etc.). L'existence d'une seule vertèbre fulcrale (S1) et d'une longue queue non préhensile constituent, eux, des caractères de polarité incertaine. L'articulation du tarse est de type «bicontact» comme chez les Didelphidae actuels ; en outre la facette cuboïde du calcanéum présente une orientation en partie plantaire qui peut être interprétée comme préfigurant la spécialisation des Didelphidae ultérieurs ; ce tarse est donc plus spécialisé que celui du «plesiomorphic metatherian morphotype» de Szalay (1982a,b ; 1984), ne le rappelant que par le grand processus péronéen du calcanéum et la largeur remarquable qui sépare ce processus et le bord médial du sustentaculum. Prise dans son ensemble, cette analyse du squelette soutient l'opinion, basée sur l'étude du crâne et de la denture, selon laquelle *Pucadelphys* représente le taxon plésiomorphe à l'intérieur des Didelphidae. Les considérations fonctionnelles résultant de l'étude de ces squelettes suggèrent que *Pucadelphys* était un animal essentiellement terrestre, plutôt vif et capable, dans certaines limites, de sauter aussi bien que de creuser.

RÉSUMÉ DÉVELOPPÉ

Les restes de squelettes postcrâniens des mammifères paléogènes sont extrêmement rares et, qui plus est, difficiles à identifier en raison de l'absence d'association avec les dents, organes sur lesquels est essentiellement fondée la taxonomie de ces animaux.

Or les squelettes étudiés dans cette troisième partie sont non seulement associés à des crânes munis de leur denture (voir Part. II de ce volume), mais ils sont très complets (95% des os sont représentés) et très bien conservés. Ils sont enfin les plus anciens restes squelettiques connus de marsupiaux, cette position étant jusqu'ici tenue par des os tarsiens isolés du Paléocène supérieur d'Itaboraí, Brésil.

L'étude détaillée de ces squelettes est donc du plus haut intérêt. Les comparaisons ont été faites, d'une part avec les rares squelettes connus de mammifères mésozoïques: l'éothérien *Eozostrodon*, du Jurassique inférieur d'Afrique du Sud, le thérien non tribosphénique *Henkelotherium*, du Jurassique supérieur du Portugal, et les placentaires du Crétacé inférieur de Mongolie ; avec d'autre part les petits didelphides généralisés actuels : *Metachirus, Monodelphis, Marmosa* et *Didelphis*, avec aussi *Perameles*.

La colonne cervicale de *Pucadelphys andinus* est celle d'un petit didelphide actuel, si ce n'est que l'atlas montre la persistance d'une suture entre l'intercentre et l'arc neural, et que l'axis est dépourvu de canal transverse et garde des côtes axiales, deux caractères primitifs. La colonne thoracique est non moins généralisée dans son ensemble ; par contre la colonne lombaire est interprétée comme dérivée, en raison de l'allongement progressif du corps vertébral et des apophyses transverses, et de la hauteur des épines neurales dirigées vers l'avant : une telle morphologie ne se retrouve pas chez les didelphides examinés, mais bien chez la forme fouisseuse *Perameles*. Dans ce contexte, le sacrum est considéré comme spécialisé, avec deux vertèbres dont une seulement s'appuie sur l'ilion. La longueur de la queue reste imprécise, mais les vertèbres caudales conservées ne montrent aucune spécialisation préhensile, contrairement à celles d'*Henkelotherium* ou de *Didelphis*.

La ceinture scapulaire est identique à celle des didelphides actuels les plus primitifs ; l'humérus montre une vaste surface d'insertion pour les extenseurs, comme celui des petites formes terrestres ; le cubitus et le radius sont encore très robustes. Les os du carpe et de la main n'ont pas été conservés.

La bassin, bien que massif, présente, comme le sacrum, des spécialisations de type péramélide, avec une grande expansion dorso-ventrale de l'aile antérieure de l'ilion, un grand foramen obturateur, et des os marsupiaux réduits. Au contraire, les os de la cuisse et de la jambe sont plus primitifs que ceux des petits didelphides actuels. L'astragale n'est pas très bien conservé, mais il semble que sa morphologie était plus plésiomorphe que celle de *Didelphis*. Quant au calcanéum, il est dépourvu de facette fibulaire ; il est donc plus évolué que celui définissant le "morphotype métathérien" de Szalay (1982a, b) et se rapproche du "morphotype didelphide" ; il conserve pourtant un fort processus péronéen, interprété dans ce contexte particulier comme un caractère plésiomorphe. Un point intéressant concerne l'orientation de la facette cuboïdienne, considérée comme annonçant la condition des didelphides actuels. Le pied lui-même paraît avoir été long et relativement rigide.

Source : MNHN, Paris

De l'ensemble de ces caractères, les auteurs déduisent pour *Pucadelphys andinus* un mode de vie terrestre et non arboricole (une adaptation considérée comme primitive pour les Theria Tribosphenida, KREBS, 1991) : l'astragale et le calcanéum en particulier ne montrent pas les caractères reliés à une telle spécialisation ; malheureusement la configuration de la jonction tibia-astragale n'a pu être précisée, nous ignorons donc s'il y avait renversement du pied comme observé par JENKINS & MC LEARN (1984) chez quelques didelphides arboricoles.

Dans le détail, la brièveté des apophyses épineuses des vertèbres cervicales suggère une bonne mobilité du cou. L'étroitesse de l'espace séparant radius et cubitus imposait une rotation limitée de l'avant-bras. Le développement des métapophyses dorsales, la longueur des apophyses épineuses des vertèbres lombaires et la largeur de l'extrémité distale de l'humérus constituent autant de potentialités fouisseuses ; de même, la longueur des épines lombaires et la conformation du sacrum (possible mobilité de la jonction sacro-iliaque, grand angle ilio-sacré, largeur et orientation de la surface iliaque destinée aux abducteurs et extenseurs de la cuisse) devaient favoriser le fouissement, sans qu'une telle spécialisation soit, chez *Pucadelphys,* poussée aussi loin que chez *Perameles*. Par ailleurs les proportions relatives des membres supérieur et inférieur sont compatibles avec une bonne agilité mais ne correspondent pas à celles d'un animal coureur ; enfin cette espèce semble avoir été capable de sauter, mais sans être réellement spécialisée dans cette direction.

En ce qui concerne le mode de vie, cette forme devait être nocturne comme la plupart des petits didelphides, dormant le jour dans un nid-terrier et cherchant sa nourriture durant la nuit. La connaissance des mœurs des petits didelphides actuels (qui sont habituellement solitaires) conduit à penser que ces quatre squelettes associés deux à deux représentent ceux de couples formés durant la période de reproduction ; les terriers étaient creusés dans la berge d'une rivière, dont la crue subite a rempli ces nids de sédiments ayant favorisé la conservation en position naturelle. Cette conclusion est corroborée par l'abondance des fossiles trouvés dans le gisement (comportant en particulier des squelettes presque complets de grenouilles).

Peu de caractères du squelette permettent de préciser la position phylogénique de *Pucadelphys andinus*, si ce n'est la configuration du tarse. Celle-ci, jointe aux conclusions concernant le crâne et la denture, font considérer *Pucadelphys* comme le taxon le plus plésiomorphe à l'intérieur des Didelphidae.

INTRODUCTION

Postcranial bones of mammals are very important in phylogenetic studies; yet these elements are extremely rare in rocks of Cretaceous and Paleocene age, a time when the basic branches of this class became established. Associated skeletons which provide functional and phylogenetic information are even rarer, and those with associated dentitions and skulls are almost non-existent. Because of a dearth of such specimens, little is known of the early postcranial evolution of Tribosphenida (metatherians, eutherians and related forms with tribosphenic dentitions; *sensu* MCKENNA, 1975). In fact, the postcranial character states in the direct ancestor(s) of metatherians and eutherians are currently inferred from the study of all too few isolated Cretaceous and Paleocene elements, of Eocene to Pleistocene fossils, and of living taxa.

There are, to date, only two non-tribosphenid therians (both eupantotheres) for which associated postcranial material is known. One is *Henkelotherium guimarotae* from the Late Jurassic of Portugal, described by KREBS (1987; 1991), and the other is *Vincelestes neuquenianus* from the Early Cretaceous of Argentina, which is not yet described (see BONAPARTE & ROUGIER, 1987 ; ROUGIER *et al.*, 1992 ; WIBBLE & HOPSON, 1993).

Eutherians are the best known of Late Cretaceous tribosphenids, and partial skeletons of *Asioryctes, Zalambdalestes* and *Barunlestes* have been described from the ? Late Santonian and/or Campanian of Asia (KIELAN-JAWOROWSKA, 1977, 1978).

In contrast, postcranial remains of metatherians from the Late Cretaceous and Paleocene are presently known only from isolated calcanea and astragali (SZALAY, 1982a and b; 1984); associated skeletons have not been reported. The earliest nearly complete skeleton of a metatherian

Source : MNHN, Paris

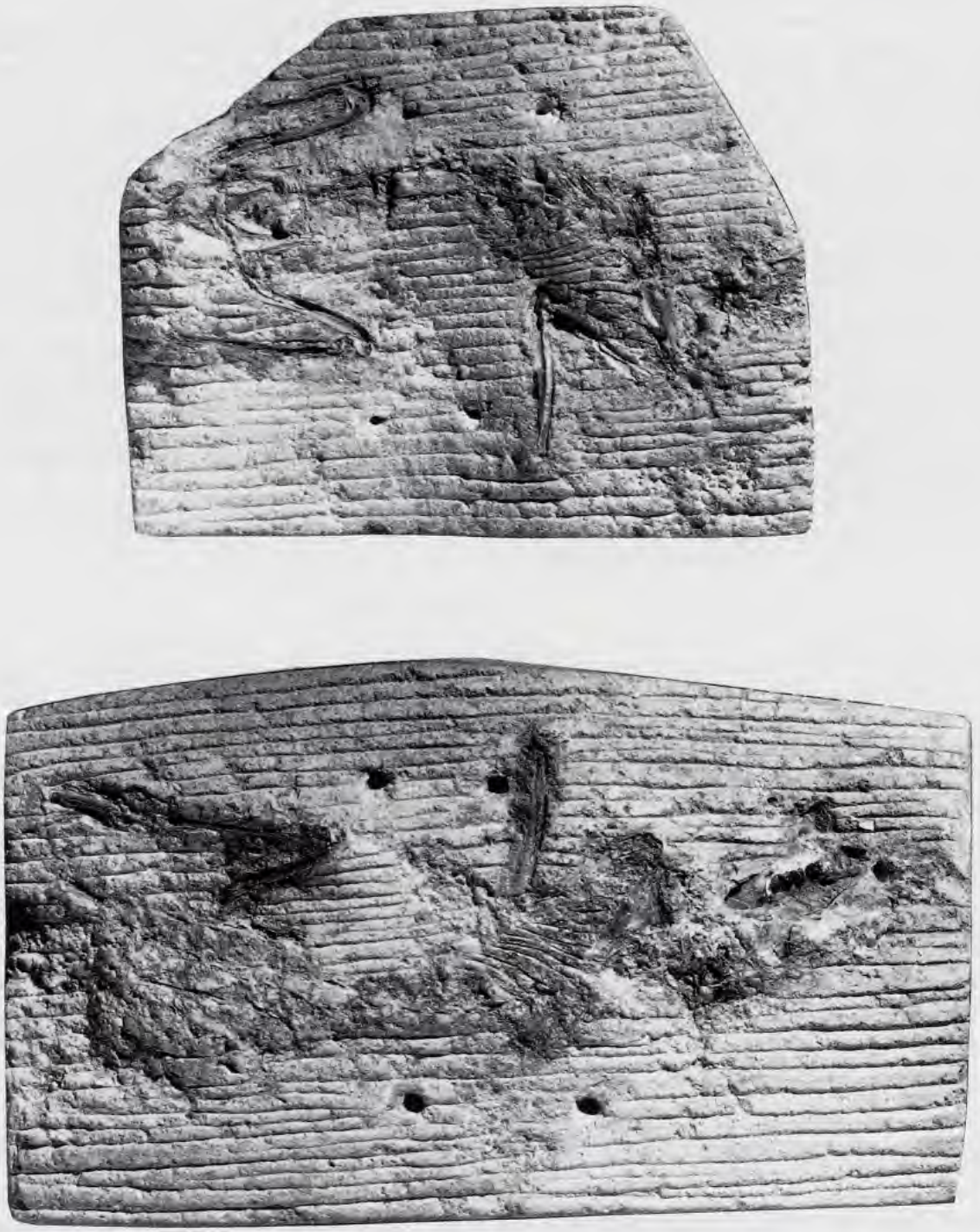


FIG. 22. — The "sarigue fossile" from Montmartre, CUVIER collection MNHN 7905 (top) and 7904 (bottom): opposite halves of same specimen, type of *Peratherium cuvieri* Fischer, 1829. X 1.

FIG. 22. — La sarigue fossile de Montmartre, collection CUVIER MNHN 7905 (haut) et 7904 (bas): moitiés opposées du même spécimen, type de Peratherium cuvieri *Fischer, 1829. X 1.*

Source : MNHN, Paris

FIG. 23. — The "sarigue fossile" from Montmartre (after CUVIER 1804, Pl. 19), type of *Peratherium cuvieri* (Fischer, 1829).

FIG. 23. — La sarigue fossile de Montmartre (d'après CUVIER 1804, Pl. 19), type de Peratherium cuvieri *(Fischer, 1829).*

Source : MNHN, Paris

was long represented by the classic "sarigue fossile" collected from the Butte Montmartre in northcentral Paris (Figs 22, 23). The fossil is from the "Gypse de Montmartre", assigned to the Late Eocene (*i.e.* Headonian Land Mammal Age, SAVAGE *et al.*, 1994). It was first described by CUVIER (1804), named *Didelphis cuvieri* by FISCHER (1829), and is now classified as *Peratherium cuvieri* (CROCHET, 1980).

Hence the major interest of the four nearly complete skeletons, two of which have articulated skulls, of the metatherian *Pucadelphys andinus*, from the Early Paleocene Santa Lucía Formation at Tiupampa in southcentral Bolivia. These are currently the earliest and most complete articulated skeletons of metatherians yet known, and they provide the first opportunity to securely assess aspects of the postcranial structure of a member of this group at the "Beginning of the Age of Mammals".

Unless otherwise specified, all numbers cited below, in the figure captions and in the Appendix (i.e. 6105, 6106, 6110, 6111) pertain to YPFB.

SYSTEMATIC PALEONTOLOGY

The skeleton-pairs described in this study were collected with articulated skulls, one of which (6105) was designated the type of *Pucadelphys andinus* MARSHALL & MUIZON, 1988. A detailed study of the dentitions and skulls of 6105 and 6110 (as well as numerous other specimens), shows that both skeleton-pairs are referable to this species (MARSHALL & MUIZON, 1995). The systematic position of the skeletons is thus as follows:

Legion TRIBOSPHENIDA McKenna, 1975
Infraclass METATHERIA Huxley, 1880
Order DIDELPHIMORPHIA (Gill, 1872) Marshall *et al.*, 1989
Family DIDELPHIDAE Gray, 1821
Genus *PUCADELPHYS* Marshall & Muizon, 1988

Pucadelphys andinus MARSHALL & MUIZON, 1988

DIAGNOSIS (postcranial skeleton morphology only). — Atlas not perforated by transverse canal, and with a persisting suture between ossified intercentrum and atlantal arch; absence of transverse canal on axis, with possible unfused rib; absence of enclosed transverse canal on CV7; lumbar series specialized compared to that of other didelphids (gradual lengthening of vertebral body and transverse processes, long anteriorly directed neural spines); single fulcral vertebra (Sl); specialized pelvis (ilium dorsoventrally expanded anteriorly, large obturator foramen, small ossified os marsupium); possible movable sacro-iliac joint; long (±30 caudals) non-prehensile tail; digging specializations of the humerus (no third distal articular surface, large areas for extensors of forearm and carpus); robust fibula; calcaneum with bicontact upper ankle joint (UAJ) (SZALAY, 1982a, b), large peroneal process and remarkably broad transverse dimensions from peroneal process to medial margin of sustentaculum.

Source : MNHN, Paris

DESCRIPTION

Measurements (in mm) of the individual bones of the specimens of *Pucadelphys* described below are given in Tables 1 to 20 in the Appendix.

General Features. — Skeleton-pairs YPFB Pal 6105 and 6106 (Figs 2, 24A and 25A). The animals are in a snout-rump position; 6105 faces to the right and 6106 to the left (referring to the positions as in the photos). Part of the dorsal surface and the entire ventral surface of both individuals are presently visible, and the latter was presumably on the floor of the burrow when the animals died and were fossilized. Both individuals are adults as evidenced by the facts that the skull of 6105 has a slightly worn adult dentition and the epiphyses, although still distinct, are all firmly attached to the diaphyses. 6106 is slightly larger than 6105 (see Appendix).

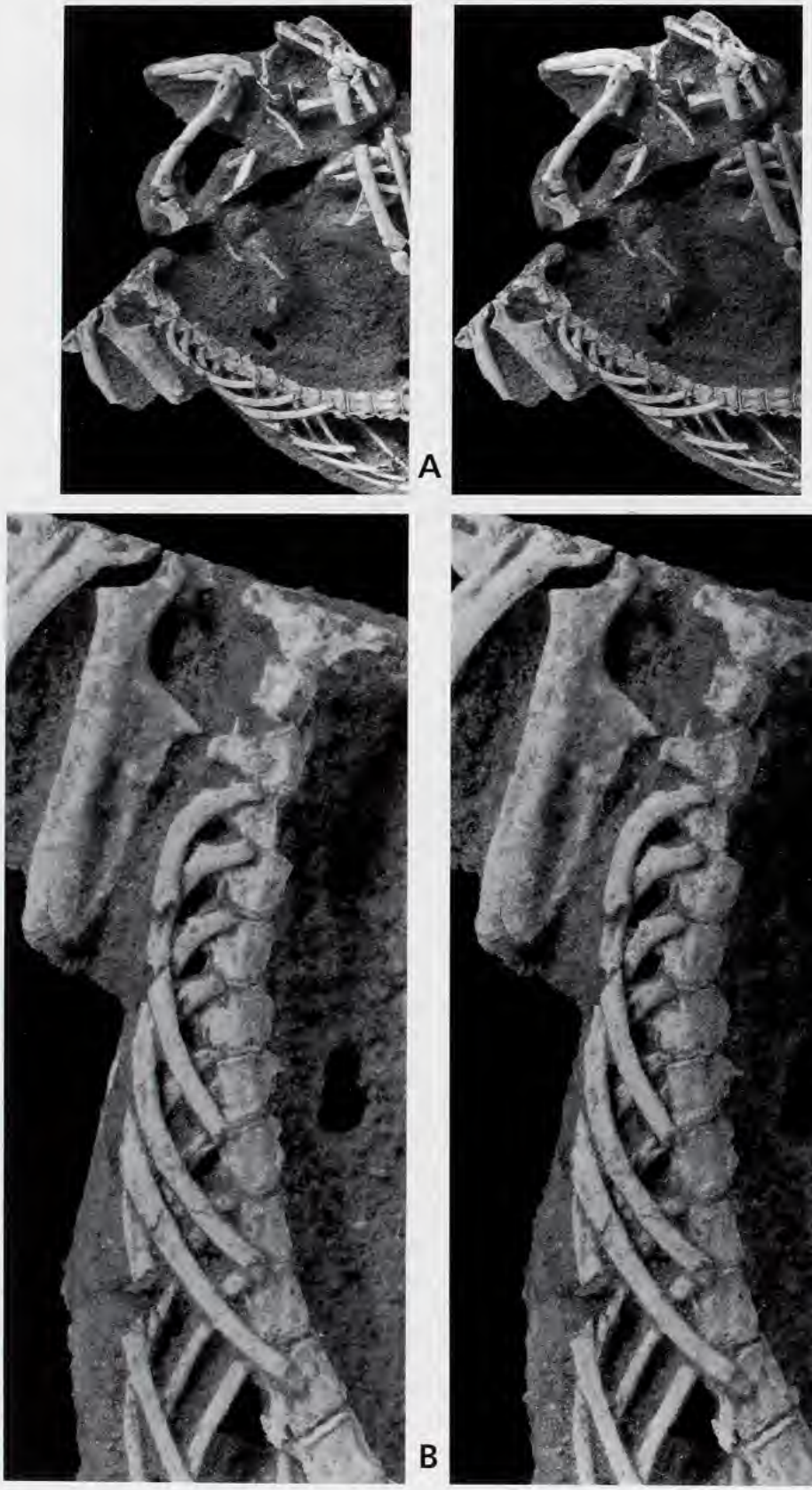
On 6105, the seven cervical and eleven thoracic vertebrae are in a nearly straight line. The left forelimb is extended posteriorly and parallel along the body. The left hindlimb (as seen on the opposite surface of the block) has the femur on top of the thoracic region of 6106, the tibia and fibula extend posteriorly over the thoracic vertebrae to T11, and the pes is on the right side of that specimen. These features indicate that the pelvic region of 6105 was lying upon the upper thoracic, neck and possibly head region of 6106.

On 6106, the body is in an arched position as shown by the arrangement of the articulated T1 to C9 vertebrae. The right forelimb lies along side and nearly parallel to the body and, as shown by the humerus, was extended posterolaterally. The proximal part of the left forelimb is extended anterolaterally under the posterior lumbar-pelvic region of 6105, with the ulna and radius flexed sharply anteriorly along the posterolateral side of 6105. The right hindlimb is flexed anteriorly under the abdominal area. The left hindlimb is extended laterally, with the tibia and fibula under the thoracic region of 6105.

Skeleton-pairs YPFB Pal 6110 and 6111 (Figs 3, 4 and 26). The animals are also in a snout-rump position; 6110 faces to the right and 6111 to the left (referring to the positions as in the photos). The dorsal surfaces of both individuals are visible. Both individuals are subadults as demonstrated by the facts that the skull of 6110 has an unworn adult dentition and the epiphyses are unfused and often separated from the diaphyses in both individuals. 6110 is slightly larger than 6111 (see Appendix) and both individuals are notably smaller (average about 20%) than 6105 and 6106.

On 6110, the pelvic area is nearly horizontal. The tail bends sharply dorsolaterally to the left and the end of the tail lies upon, and parallels, the thoracic vertebrae of 6111. In the posterior thoracic region the body begins to twist to the left, with the cervicals and head completely on their left side. The proximal end of the right forelimb is extended posterolaterally and the ulna is flexed sharply anteriorly. The left forelimb extends parallel along the posterior side of the proximal part of the right forelimb. The relationship of the forelimbs and cervical vertebrae clearly shows that the animal was lying on its left shoulder. The right hindlimb was extended nearly perpendicular to the body, while the left hindlimb was in a tightly anteriorly flexed position directly under the body.

Source : MNHN, Paris



Source : MNHN, Paris

6111 was lying on its right shoulder with the right forelimb extending nearly perpendicular on the left side of the body (as seen by the position of the distal end of the humerus and proximal ends of the ulna and radius). The left forelimb was flexed tightly against the thoracic region of the right side of the body and the "elbow" abuts vertebrae T8 and T9. The proximal end of the right hindlimb extends anteriorly under the body such that the femur parallels the lumbar vertebrae and the distal end (tibia and fibula) extends nearly perpendicular on the left side of the body. The left hindlimb is extended anterolaterally on the left side of the body, and the distal parts of the tibia and fibula (and pes) lie upon the lumbar region of 6110.

Collectively, the four specimens include about 95% of the complete skeleton. The only missing elements are the manus (see p.127), the first metatarsal, some tarsals and phalanges of the pes, and an estimated 17 posterior caudal vertebrae.

AXIAL SKELETON.

6105	7 cervicals (left half of atlas, axis, CV3-CV7) 9 thoracics (T1-T9, fragments of T10-T11)
6106	13 thoracics (T1-T13) 6 lumbars (L1-L6) 2 sacrals (S1-S2) 9 caudals (C1-C9)
6110	7 cervicals (atlas, axis, CV3-CV7) 8 thoracics (T6-T13) 6 lumbars (L1-L6) 2 sacrals (S1-S2) 9 caudals (C1-C5, C16?-C17?, C20?-C21?)
6111	7 thoracics (T7-T13) 6 lumbars (L1-L6) 2 sacrals (S1-S2) 9 caudals (C1-C9)

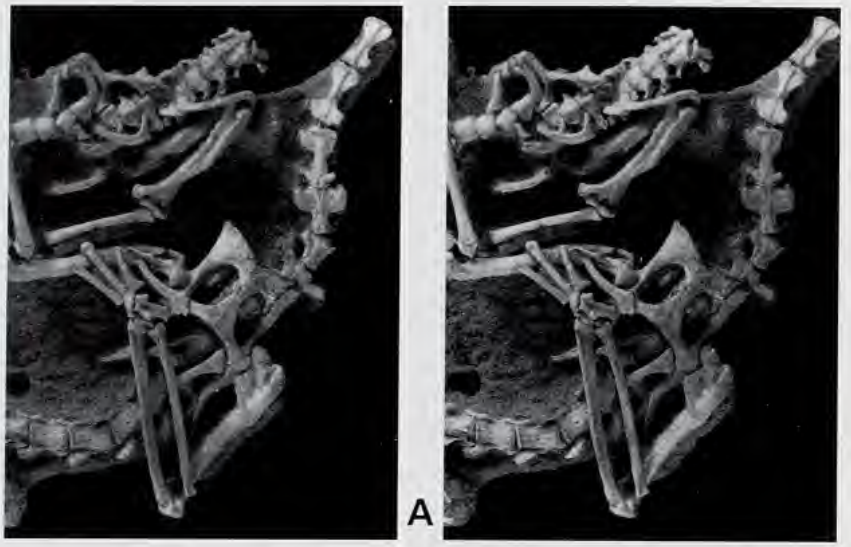
CERVICAL VERTEBRAE

Atlas (Figs 25B, 27 and 28A, B; Table 1).— Two elements: 6105, left half (attached to axis), ventral and lateral views; 6110, isolated left and right halves, nearly complete.

FIG. 24. — *Pucadelphys andinus*. Stereophotos. A, specimen-pair 6105-6106, partial view. X 1; B, 6106, right scapula, anterior view; thoracic vertebrae and ribs, ventral view. X 3.

FIG. 24. — Pucadelphys andinus. *Stéréophotos. A, couple des spécimens 6105-6106, vue partielle. X 1; B, 6106, omoplate droite, vue antérieure; vertèbres thoraciques et côtes, vue ventrale. X 3.*

Source : MNHN, Paris



A

B

Source : MNHN, Paris

The dorsal arch (da) is narrow ventrally and considerably broader dorsomedially. Laterally, the dorsal arch joins the base of the ventral arch and projects as a flat, horizontal, ovoid transverse process (6105), constricted at the base. In 6110, only the root of the transverse process is preserved on both halves (b tp); but the lateral-most surface does not appear to be broken, suggesting that the transverse process had a different center of ossification and fused with the root only in adults. Anterior to the transverse process, the articular facet for the occipital condyle (lf of) is wide and distinctly concave; posterior to it, the articular facet for the atlas body (i.e. anterior part of the axis *sensu lato*) is smaller and only slightly concave (ax f). The two articular facets (for occipital and atlas body) are not situated directly opposite each other anteroposteriorly: the occipital facet slopes posteromedially at an angle of about 40°, while the atlas body facet is more transverse and faces mostly posterolaterally at an angle of about 33°. As for the ventral component of the atlas (intercentrum), what must be its lateral part appears to be suturally joined to the left atlas of 6105 and directed towards the ventral surface of the dens. Supporting this interpretation is the presence of a facet on the posteroventromedial edge of the atlas arch of 6110, immediately adjacent to the articular facet for the atlas body of the axis (Fig. 27C, si); we thus assume that the intercentrum was ossified in the adult. The groove for the vertebral artery at the anterior base of the dorsal arch is deep in the adult 6105 and shallower in the subadult 6110 (t s). Behind the transverse process, a deeper sulcus (for "neuro-vascular structures" according to JENKINS & PARRINGTON, 1976) separates the latter from the axial facet. A very small canal is clearly visible on the right side of 6110 (t c?), the posterior opening of which, just behind the root of the transverse process, being larger than the anterior one which is in front of the same process; whether this is homologous to a transverse canal remains uncertain (see discussion p. 111). The atlantal canal for cranial nerve I, situated on the medial side of the occipital facet, is not closed.

Axis (Figs 25, 28C-E, 29A and 38A; Table 1). — Two elements: 6105, ventral, medial and left lateral views; 6110, all surfaces visible.

The suture between the atlantal and axial component is distinct in 6110 on the dorsal and ventral surface of the body, while in 6105 it only appears as an elevated transverse ridge on the ventral surface, but is still distinct on the dorsal surface. The atlas component of the axis body is wider than the axial part. Both components have two (paired) distinct nutrient foramina on the dorsal face of the body. The dens is oriented anterodorsally, is slightly flattened dorsoventrally, and transversely convex both dorsally and ventrally. A distinct medial keel extends longitudinally along the ventral surface of the body and posteriorly forms a broad lip. Lateral to the medial keel are two broad depressions which are bordered by the ventral root of the transverse processes (Fig. 28, tp v). The neural arch (6105) is very long dorsally relative to its ventral base; hence the anterior

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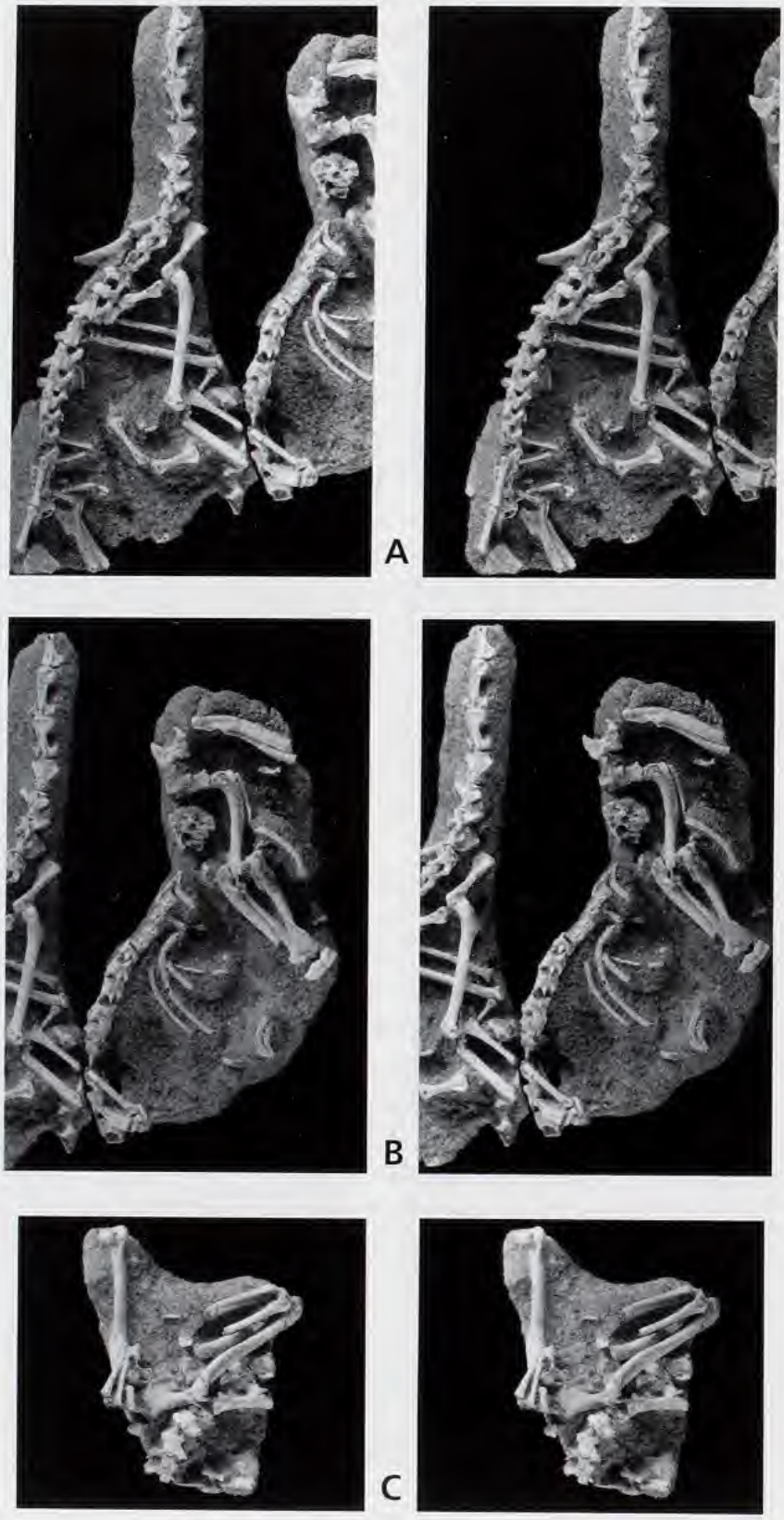
FIG. 25. — *Pucadelphys andinus*. Stereophotos. A, specimen-pair 6105-6106, partial view. X 1; B, 6105, cervical vertebrae, interclavicle and left clavicle, ventral view. X 3.

FIG. 25. — Pucadelphys andinus. *Stéréophotos. A, couple des spécimens 6105-6106, vue partielle. X 1; B, 6105, vertèbres cervicales, interclavicule et clavicule gauche, vue ventrale. X 3.*

Source : MNHN, Paris



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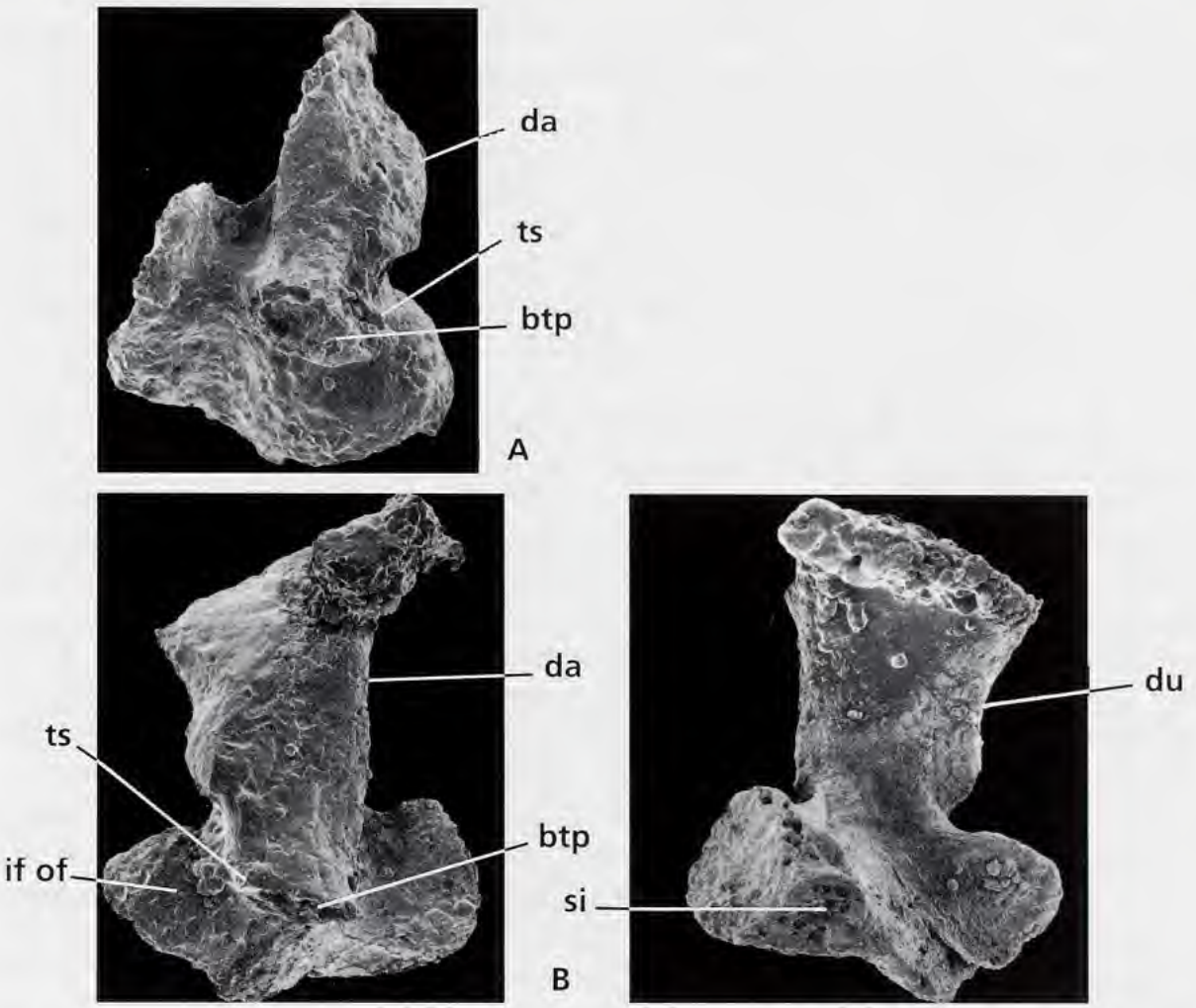


FIG. 27. — *Pucadelphys andinus*. 6110, atlas: A, right half, lateral view; B, left half, dorsolateral view; C, left half, mesial view. X 13.5. Abbreviations: **b tp**, base of transverse process; **d a**, dorsal arch; **lf of**, lateral face of occipital facet; **si**, surface for intercentrum; **t s**, transverse sulcus.

FIG. 27. — Pucadelphys andinus. *6110, atlas: A, moitié droite, vue latérale; B, moitié gauche, vue dorso-latérale; C, moitié gauche, vue mésiale. X 13,5. Abréviations:* ***b tp****, base du processus transverse;* ***d a****, arc dorsal;* ***lf of****, face latérale de la facette occipitale;* ***si****, surface pour l'intercentre;* ***t s****, sillon transverse.*

FIG. 26. — *Pucadelphys andinus*. Stereophotos. A, specimen-pair 6110-6111, partial view. X 1; B, the same, partial view. X 1; C, 6110, posterior vertebrae and hindlimb: this block appeared to represent the posterior part of 6110 only after preparation; but the ventral surface of this block had been prepared, while on the main block the preparation was of the opposite surface; in order to link the two blocks, it is necessary to reverse C and also turn it 90° (see Figs 3 and 4). X 1.

FIG. 26. — Pucadelphys andinus. *Stéréophotos. A, couple des spécimens 6110-6111, vue partielle. X 1; B, le même, vue partielle. X 1; C, 6110, vertèbres postérieures et membre postérieur: ce bloc ne s'est révélé représenter la partie postérieure de 6110 qu'après préparation; mais c'est la surface ventrale de ce bloc qui avait été préparée, alors que sur le bloc principal la préparation portait sur la face opposée; afin de relier les deux blocs, il a donc été nécessaire de renverser C et de le tourner de 90° (voir figs 3 et 4). X 1.*

Source : MNHN, Paris

border is deeply concave and the atlanto-axial intervertebral space is large. The posterior border of the neural arch is straight. The spine itself is not intact but was low, long and thin; anteriorly it overhangs the vertebral body (dens not included); posteriorly it only slightly overhangs CV3. The anteriorly facing atlantal facets (at f) are oval, short and directed almost vertically. The postzygapophysial facets face lateroventrally. The transverse process had two roots which, as seen on 6105, did not unite laterally; as a result the transverse "canal" between the two roots remains a wide sulcus (t s). The lateral extremity of the dorsal root on both sides of 6105 is uniformly concave and does not appear to have been broken; this may have been the attachment surface for a small cervical rib, a remnant of which may be represented by the bone fragment located along the anterior surface of the dorsal root of CV3 of 6105.

Cervicals 3 to 7 (Figs 25, 28D-E and 29A; Table 2). — Two series: 6105, CV3-7; 6110, CV3-7 (fragmentary).

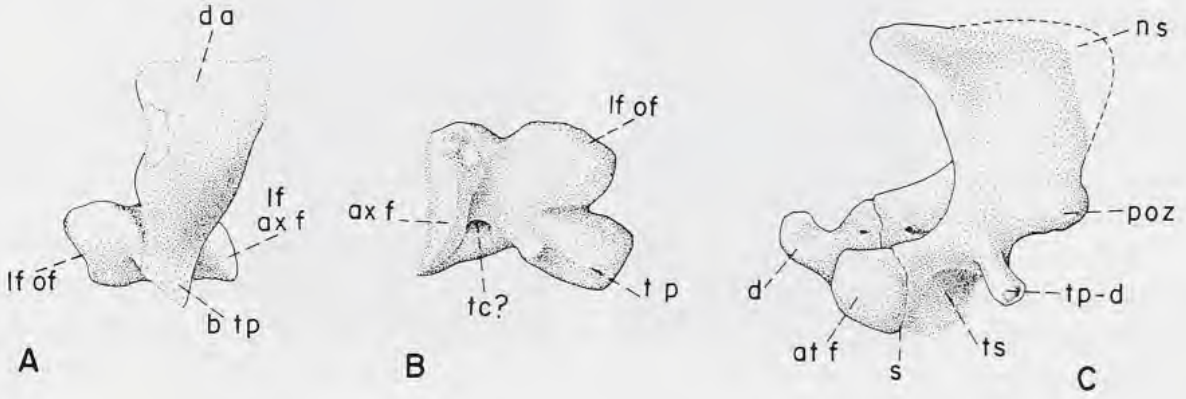
The epiphyses on all elements remain distinct. CV3 is notably longer than CV4 and both are slightly larger than CV5-CV7, which are also subequal in length. The intervertebral spaces narrow from CV3 to CV7. The zygapophysial facets are only slightly inclined lateroventrally on CV3, and become nearly horizontal on CV4 (not preserved on CV5 to CV7). The vertebral bodies are low and wide, and the spine was apparently short (only the base is preserved on CV3-CV5). The two roots of the transverse process of CV3 to CV6 unite laterally, enclosing the transverse canal (t c); together they produce a thick posterior process, while the ventral root has also an anteroventral projection or tubercle (t). There are no free cervical ribs.

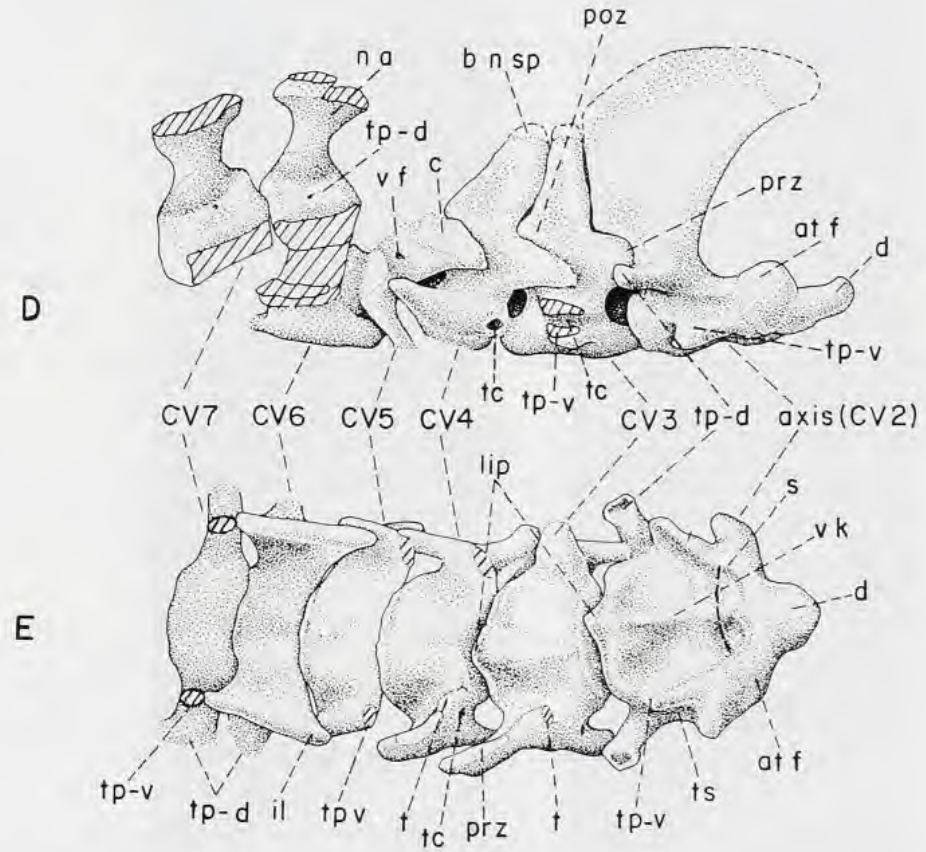
CV3 has a distinct median ventral keel which broadens posteriorly and ends in a wide lip; a nutrient foramen pierces the base of the keel. The lateral depressions are well developed, but shallower than those on the axis. The anterior projection of the ventral root of the transverse process is reduced to a tubercle (Fig. 28E, t). The spinous process is nearly vertical, very short, and the anterior border of the arch is closely appressed to the posterior border of the axial arch, suggesting that there may have been some contact between the two arches.

FIG. 28. — *Pucadelphys andinus*. A-B, atlas: A, 6110, left half, dorsolateral face; B, 6105, left half, ventral face; C, 6110, axis, left lateral face; D-E, 6105, cervical vertebrae CV2-CV7: D, right lateral face; E, ventral face. All drawn as preserved. X 8. Abbreviations: **at f**, atlantal facet; **ax f**, axial facet; **b n sp**, base of neural spine; **b tp**, base of transverse process; **d**, dens; **d a**, dorsal arch; **il**, inferior lamella of CV6; **lf ax f**, lateral face of axial facet; **lf of**, lateral face of occipital facet; **n a**, neural arch; **n s**, neural spine; **poz**, postzygapophysis; **prz**, prezygapophysis, **s**, suture between atlantal and axial component; **t**, tubercle, see text; **tc**, transverse canal; **t p**, transverse process, **tp-d**, dorsal root of transverse process; **tp-v**, ventral root of transverse process; **ts**, transverse sulcus; **v f**, vascular foramen; **v k**, ventral keel.

*FIG. 28. — Pucadelphys andinus. A-B, atlas: A, 6110, moitié gauche, face dorso-latérale; B, 6105, moitié gauche, face ventrale; C, 6110, axis, face latérale gauche; D-E, 6105, vertèbres cervicales CV2-CV7: D, face latérale droite; E, face ventrale. Dessin en l'état de conservation. X 8. Abréviations: **at f**, facette atlantale; **ax f**, facette axiale; **b n sp**, base de l'épine neurale; **b tp**, base du processus transverse; **d**, dens; **d a**, arc dorsal; **il**, lamelle inférieure de CV6; **lf ax f**, face latérale de la facette axiale; **lf of**, face latérale de la facette occipitale; **n a**, arc neural; **n s**, épine neurale; **poz**, postzygapophyse; **prz**, prézygapophyse; **s**, suture entre les composants atlantal et axial; **t**, tubercule, voir texte; **tc**, canal transverse; **t p**, processus transverse; **tp-d**, racine dorsale du processus transverse; **tp-v**, racine ventrale du processus transverse; **ts**, sillon transverse; **v f**, foramen vasculaire; **v k**, carène ventrale.*

Source : MNHN, Paris





Source : MNHN, Paris

CV4 has a broad, low, median ventral thickening that widens considerably posteriorly (it is nearly as wide as the posterior epiphysis); the lateral depressions are thus reduced and very shallow. The anterior tubercle of the ventral root of the transverse process is quite prominent. The neural arch is similar to that of CV3 and had probably some contact with that of CV2. The spine itself was very short.

CV5 is flat ventrally. The anterior tubercle of the ventral root of the transverse process is broken, but it was clearly longer than that of CV4; the dorsal root is covered by the inferior lamella (lamina ventralis) of CV6 (Fig. 28 D-E, i l). The left part of the dorsal arch is preserved (6105); its anterior and posterior borders are straight.

Between the two inferior lamellae of CV6 (the anterior part of which corresponds to the elongation of the above mentioned tubercle and the posterior part to the ventral component of the posterior process), the vertebral body is slightly concave; the expansion of the dorsal root of the transverse process is here separated from its ventral counterpart and is oriented more laterally than posteriorly.

On CV7, the ventral surface of the centrum has a low longitudinal median ridge and very shallow lateral depressions. The dorsal root of the transverse process is now completely laterally oriented, the ventral root is reduced to a small spine, and the two roots are not fused (i.e. the "transverse canal" is open laterally).

Thoracic vertebrae (Figs 24B, 29B, 30, 32A and 47A, B; Table 3). — Present in all four specimens: 6105, Tl to T9, ventral view (although T5 to T9 are represented only by ventral part of centra); 6106, T1 to T13, ventral and both lateral views; 6110, dorsal views of ventral half of T6 to T9, dorsal and both lateral views of T10 to T13; 6111, T12 and T13, dorsal and partial lateral views.

The presence of a small transverse process on the 14th dorsal (*i.e.* L1) demonstrates that there are 13 thoracic vertebrae.

As seen best in 6106, the vertebral body increases slightly in length from T1 to T13. T1 to T4 have a longitudinal median keel which is broad and low on Tl, higher and narrower on T2 to T4. The vertebral body is ventrally angular on T3 to T5, convex on T6 and T7, flat on T8 and T9, and with a longitudinal median trough bordered by low broad lateral ridges on T10 to T13 (a feature progressively developed from T10 to T13).

The neural spine is broken on all exposed vertebrae, except T1, T11 and T12 of 6106, and T9 and T10 of 6111 where it is low, narrow (it thickens at the top) and inclined slightly posterodorsally; it arose on the posterior half of the arch and was transversely thin at the root. The articular surfaces of the dorsal zygapophyses become more vertical posteriorly and are widely separated.

On T1 and T2, the transverse processes which bear the parapophyses for the ribs are ventrally situated opposite the anterior end of the body; they are flat and project quite far laterally, flaring slightly after a constriction at the root. Beginning on T3 they arise more medially on the body, and are also more dorsally situated due to the ventral angulation of the body; they become shorter from T5 to T7, and on T8 (and those more posteriorly), they merely constitute a less and less prominent facet on the lateral side of the body, to become undistinguishable on T11-T12.

Source : MNHN, Paris

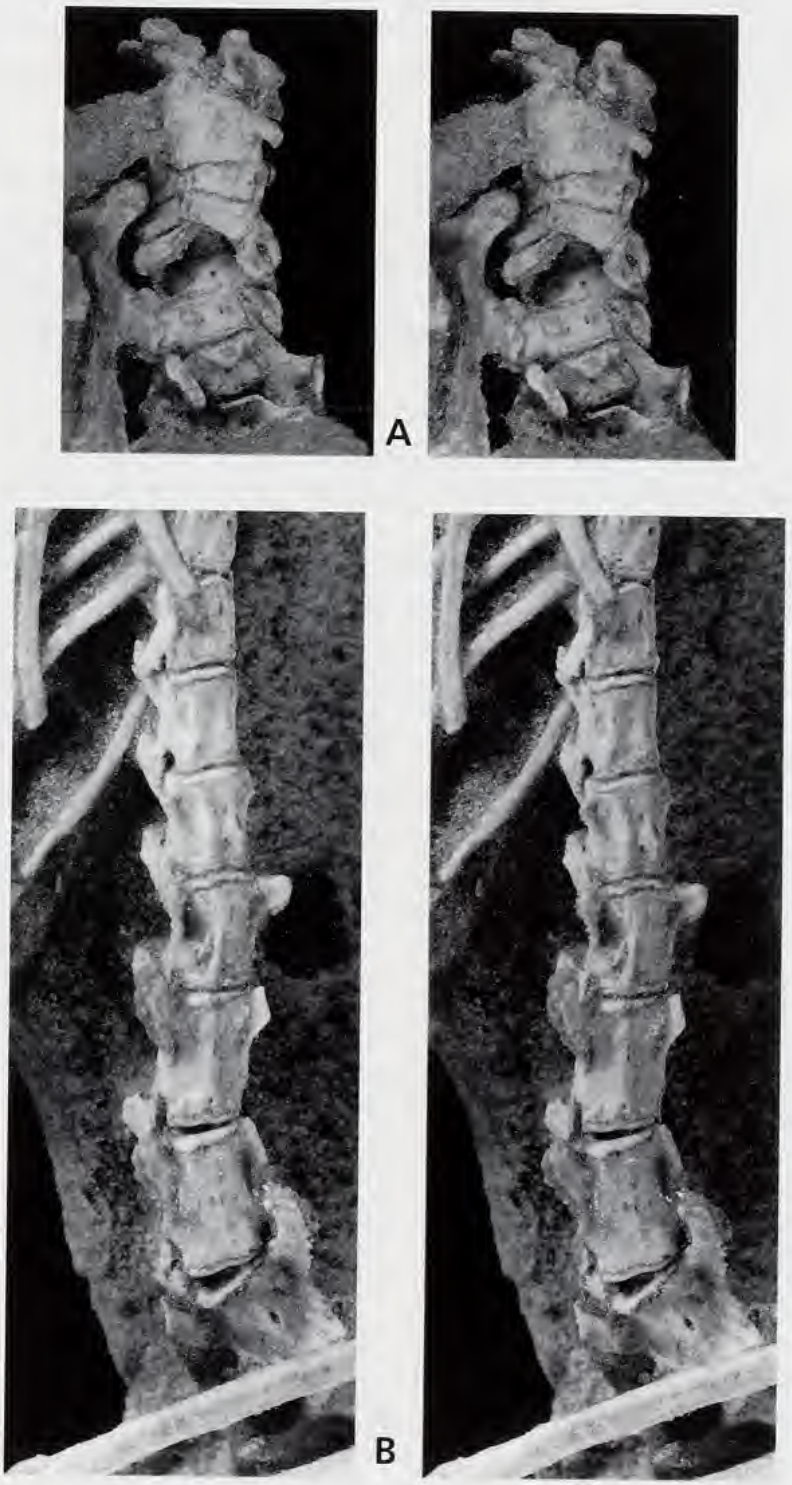


FIG. 29. — *Pucadelphys andinus*. Stereophotos. A, 6105, cervical vertebrae, dorsal view. X 3; B, 6106, vertebrae T10-L4, ventral view. X 3.

FIG. 29. — Pucadelphys andinus. *Stéréophotos. A, 6105, vertèbres cervicales, vue dorsale. X 3; B, 6106, vertèbres T10-L4, vue ventrale. X 3.*

Source : MNHN, Paris

T8 is a transitional vertebra with the appearance of the first anapophysis (ap) and the first metapophysis (mp). These apophyses become progressively longer from T9 to T13; they interlock and produce a secondary articulation at least from T10 to T13. The costal facets are not clearly discernible on the vertebral bodies.

Ribs (Fig. 24). — There are 13 pairs of ribs. The first nine pairs have tuberculae and capitulae, while the last four pairs lack tuberculae. The distal ends of all ribs are broken, so it is not possible to determine their exact length. The parts that are preserved consistently show a lack of curvature along the ventral half, indicating the presence of a relatively deep chest cavity. They are narrow, proximally compressed anteroposteriorly, with a faint longitudinal sulcus.

Lumbar vertebrae (Figs 29B, 30, 31, 32 and 41; Table 4). — Complete series (L1 to L6) in three specimens: 6106, ventral, lateral and partial dorsal views; 6110, dorsal, ventral and lateral views (L2 and L3 are damaged); 6111, dorsal, lateral and partial ventral views.

The vertebral body of the lumbars (especially of LI) is very much like that of the last thoracics, only deeper; its length increases from L1 to L4. There are usually two nutrient foramina (Fig. 32B, n f) on the ventral body surface of all lumbars, but they are more irregularly situated than those on the thoracics. The ventral surface of L1 has a shallow median longitudinal depression bordered by low broad lateral ridges, almost identical to the condition of T13; on L2 the two ridges are closer and on L3 they meet in a median longitudinal crest; L4 to L6 are gently convex transversely. The anterior and posterior rims curve slightly ventrally, producing an incipient "saddle-shape", and the body is completely platycoelous, at least posteriorly.

The neural spine, as seen on 6106, is very narrow anteroposteriorly (Fig. 31); it is dorsally directed on L1 and L2, and sharply inclined anteriorly on L3 to L6; it increases markedly in height from L1 to L4 (L4 to L6 are subequal). Due to bifurcation of the posterior base of the neural spine, the latter is more anteriorly situated on L4 to L6 and a basal sulcus develops along its posterior border.

The zygapophyses are more robust and clearly more inclined than on the thoracics, with articular facets almost vertical. The meta- and anapophyses are longer than on the thoracics, as are the "trous de conjugaison". These metapophyses are tightly interlocked with the zygapophyses (Fig. 30C).

The narrow and thin transverse processes (tv p) increase sharply in size from L1 (where they are only incipiently developed) to L6; they are inserted anteriorly on the body, all anteriorly directed, and project more and more ventrally from L2 to L6 where they make a sharp angle with the body.

Sacral vertebrae (Figs 31, 32 and 41; Table 5). — Three specimens: 6106, complete in ventral view (though slightly masked by underlying bones) and partly visible in dorsal view; 6110, ventral view of Sl and part of S2; 6111, dorsal view, but dorsal wall of vertebral body is broken on posterior half of Sl and all of S2 (thus is visible the dorsal half of the ventral vertebral body).

The sacrum consists of two vertebrae which together form a short and wide triangle ("apex" points posteriorly), but only S1 contacts the ilium (fulcral vertebra). The vertebral body

Source : MNHN, Paris

of S2 is longer than that of S1, as well as that of C1. The dorsal intervertebral foramen, elongate between L6 and S1, is very small between S1 and S2, and S2 and C1. The suture between S1 and S2 is distinct, and so is the ossification fissure between body and epiphyses.

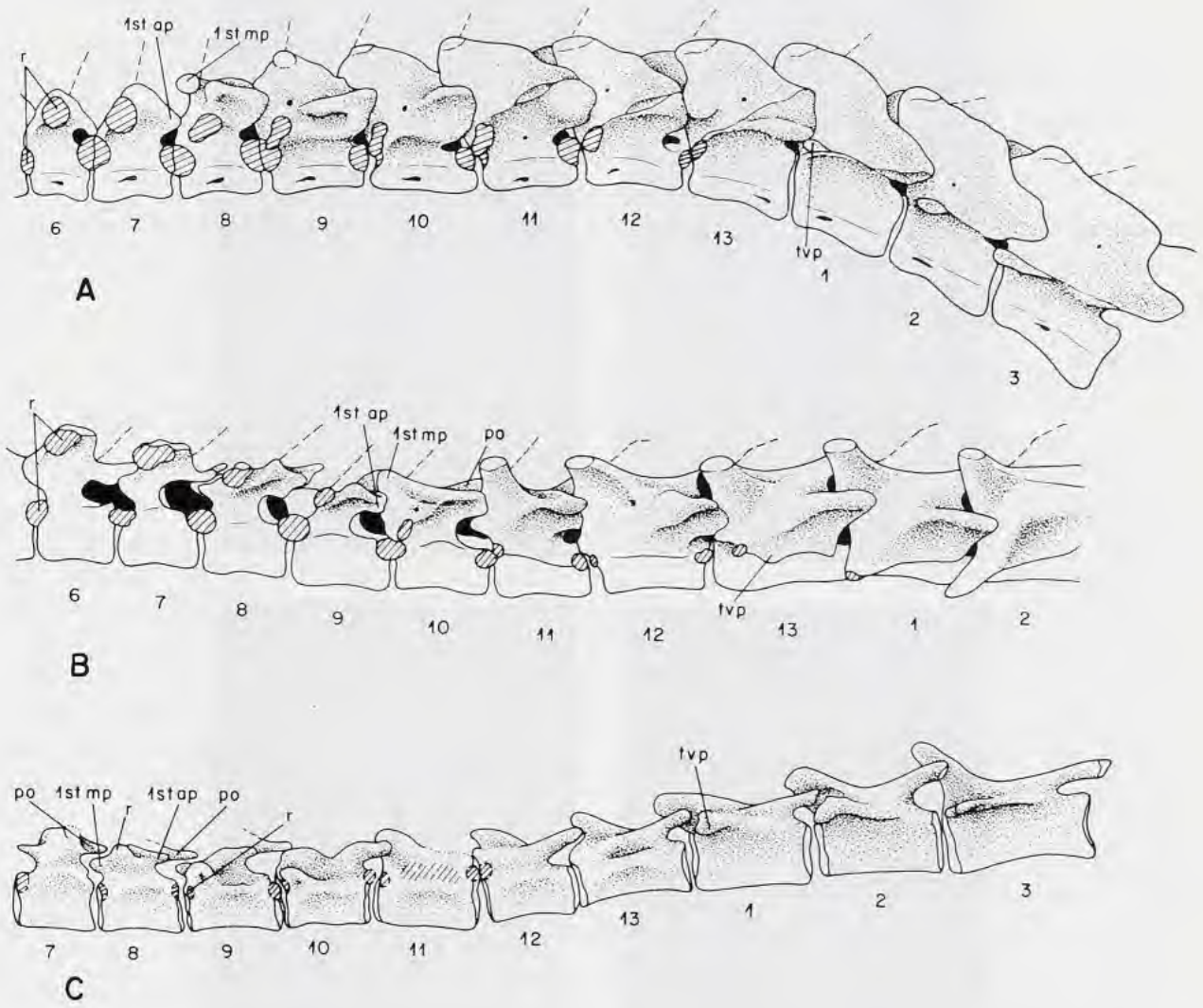


FIG. 30. — Schematic representation of thoracic and anterior lumbar vertebrae, in ventrolateral view (anterior is to left): A, *Didelphis* (MNHN A 3293 III 545), T6 to L3; B, *Metachirus nudicaudatus* (MNHN 1988-68), T6 to L2; C, *Pucadelphys andinus* (6106), T7 to L3. X 5/8. Abbreviations: **ap**, anapophysis; **mp**, metapophysis; **po**, postzygapophysis; **r**, rib attachment; **tvp**, transverse process. The dots indicate the direction of the neural spines.

FIG. 30. — Représentation schématique des vertèbres thoraciques et lombaires antérieures, en vue ventro-latérale (l'avant est à gauche): A, Didelphis *(MNHN A 3293 III 545), T6 à L3; B,* Metachirus nudicaudatus *(MNHN 1988-68), T6 à L2; C,* Pucadelphys andinus *(6106), T7 à L3. X 5/8. Abréviations:* **ap**, *anapophyse;* **mp**, *métapophyse;* **po**, *postzygapophyse;* **r**, *point d'attache des côtes;* **tvp**, *processus transverse. Les pointillés indiquent la direction des épines neurales.*

Source : MNHN, Paris

The ventral surface of the S1 vertebral body is almost flat; the sacral ribs (Fig.32, s r) flare anterolaterally, and the ends bend sharply ventrally with the lowest point at about mid-length. S2 is gently transversely convex. The transverse process of S1 flares anterolaterally and fuses with a posterior extension of the S2 transverse process, thus closing laterally the sacral foramen (s f).

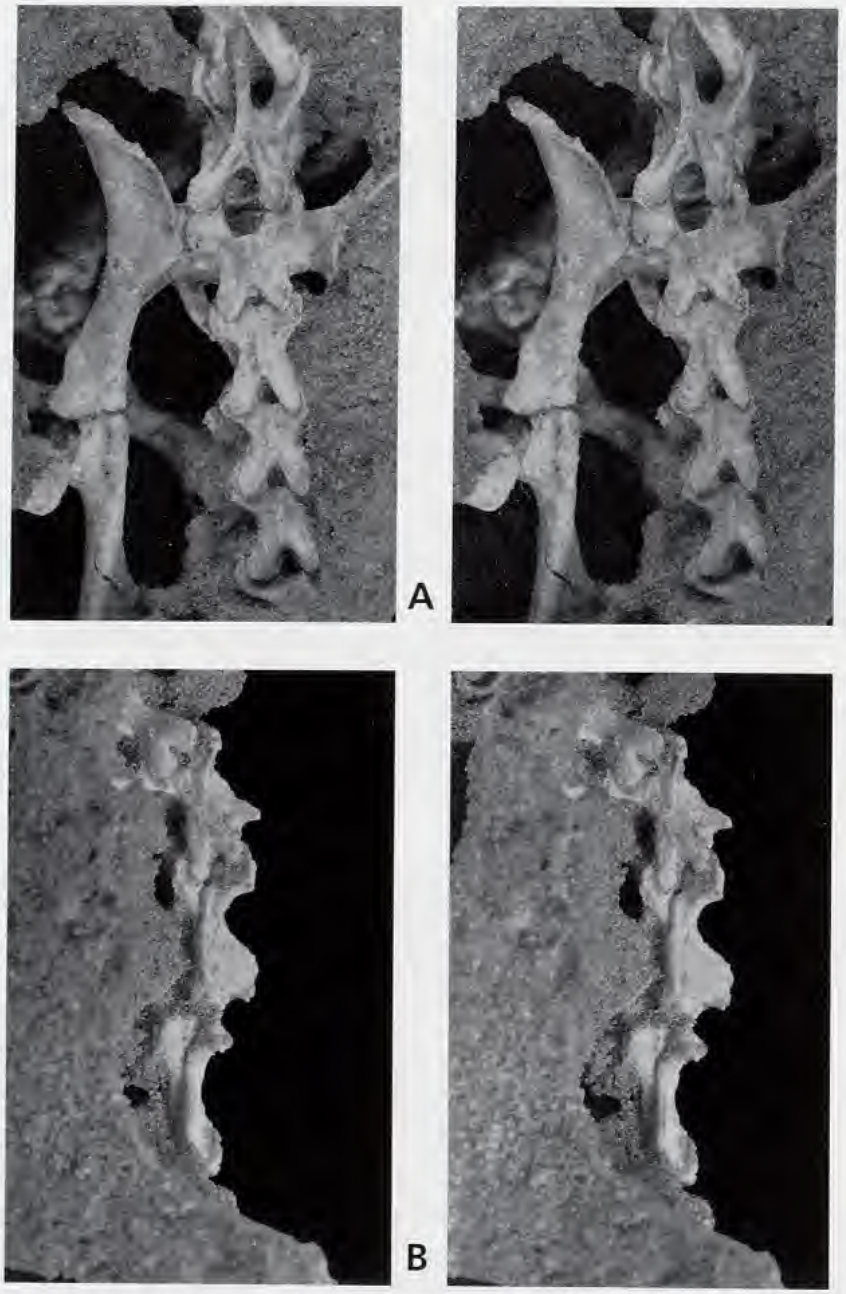


FIG. 31. — *Pucadelphys andinus*. Stereophotos. A, 6106, vertebrae L6-S1-S2, C1-C2 and left side of pelvis, dorsal view. X 3; B, 6106, vertebrae C4-C7, dorsal view. X 3.

FIG. 31. — Pucadelphys andinus. *Stéréophotos. A, 6106, vertèbres L6-S1-S2, C1-C2 et côté gauche du bassin, vue dorsale. X 3; B, 6106, vertèbres C4-C7, vue dorsale. X 3.*

Source : MNHN, Paris

The latter is subcircular, surrounded anteriorly and laterally by S1, and posteriorly by S2. Two nutrient foramina occur on the ventral body surfaces of S1 and S2. The ilio-sacral angle is estimated to have been around 15°.

Dorsally on Sl, the prezygapophyses are expanded as two widely separated wings; on S2 they are smaller, slightly closer to each other and, above all, not so ventrally flared. Still dorsally and behind the prezygapophyses, the base of the Sl transverse process is marked by a thick ridge, almost a step, oblique anterolaterally; lateral to it flares the thin sacral rib.

The base of the neural spine is preserved on S1 and S2; on S1 it extends along nearly the entire length of the arch, with the main part located at the posterior end; the spine was probably of moderate height and directed dorsally. On S2 the spine is very reduced and situated at the extreme posterior end only. On both S1 and S2 it is very thin transversely.

Caudal vertebrae (Figs 31, 33A and 34; Table 6a and b). — Represented in three specimens: 6106, C1 to C9, ventral view; 6110, C1 to C5, ventral view, C4 to C5, lateral view, C16?, ventral view, C17?, lateral, dorsal and ventral views, C20? and C21?, lateral, dorsal and ventral views; 6111, C1 to C9, dorsal view (C1 is fragmentary).

C1 to C5 are anterior caudals (*i.e.* those with zygapophyses), C6 is transitional, and C7 is the first posterior caudal. There were no haemal apophyses.

The lengths of the vertebral body on C1 to C4 are subequal in 6106 (and are all shorter than S2); beginning with C5 there is a notable elongation. Ventrally the vertebral body of C1 to C3 has a broad median longitudinal sulcus bounded laterally by low broad ridges; C4 and C5 have a low broad median ridge which flares posteriorly (on C5 it is more rounded); the longitudinal median ridge becomes narrower on C6 and C7, and more elevated on C8 and C9. The anterior and posterior epiphyses remain distinct ventrally and dorsally.

The neural spine of C1 (6106) is very short and narrow, located at the posterior end of the arch, and directed posterodorsally; on C2 none is detectable; C3 is not visible; there is apparently no spine on C4 and C5; from C6 to C9 the fused zygapophyses form a very low but long keel. Pre- and postzygapophyses are functional on C1 to C5, and prezygapophyses only on C6; they remain oblique; C7 has only tubercles that do not contact the preceding vertebra; ana- and metapophyses persist and interlock until C5 or C6.

The transverse processes (Figs. 31, 33 t p) on C1 to C3 are broad, situated at mid-length of the body, and are nearly perpendicular to the latter; on C4 and C5 they arise posteriorly on the body and flare posterolaterally; on C6 the body is narrow anteriorly and the transverse processes are broad and "wing-like" along the posterior part of the body; on C7 these posterior transverse processes are reduced, and there appear narrower, posterolaterally directed, anterior transverse processes; on C8 and C9, these anterior components have the lateral edges bent ventrally and they are slightly broader than the posterior components, which are reduced to lateral expansions.

The vertebral body of C16? to C21? consists of an elongate rod with greatly reduced anterior and posterior transverse processes; it decreases in width (but not length) from C16 to C21.

Discussion

Comparisons with *Eozostrodon-Megazostrodon, Henkelotherium, Asioryctes* and *Barunlestes* are based, respectively, on the works of Jenkins & Parrington (1976), Krebs (1991), and Kielan-Jaworowska (1977, 1978). These taxa were chosen as out-group comparisons.

Source : MNHN, Paris

Among living didelphids, comparison was made principally with *Metachirus nudicaudatus* (subadult, last molar not fully erupted, Laboratoire de Zoologie, Mammifères et Oiseaux, MNHN, specimen no 1988-68), *Monodelphis domestica*, *Philander opossum*, *Didelphis virginiana* (old adult) and *Perameles nasuta* (this taxon is used because it shares numerous specializations of the pelvic region with *Pucadelphys* as will be demonstrated below) (specimens from the collections in the Laboratoire d'Anatomie Comparée, MNHN, Paris, nos. 1967-330, A 3307, 1900-182 and

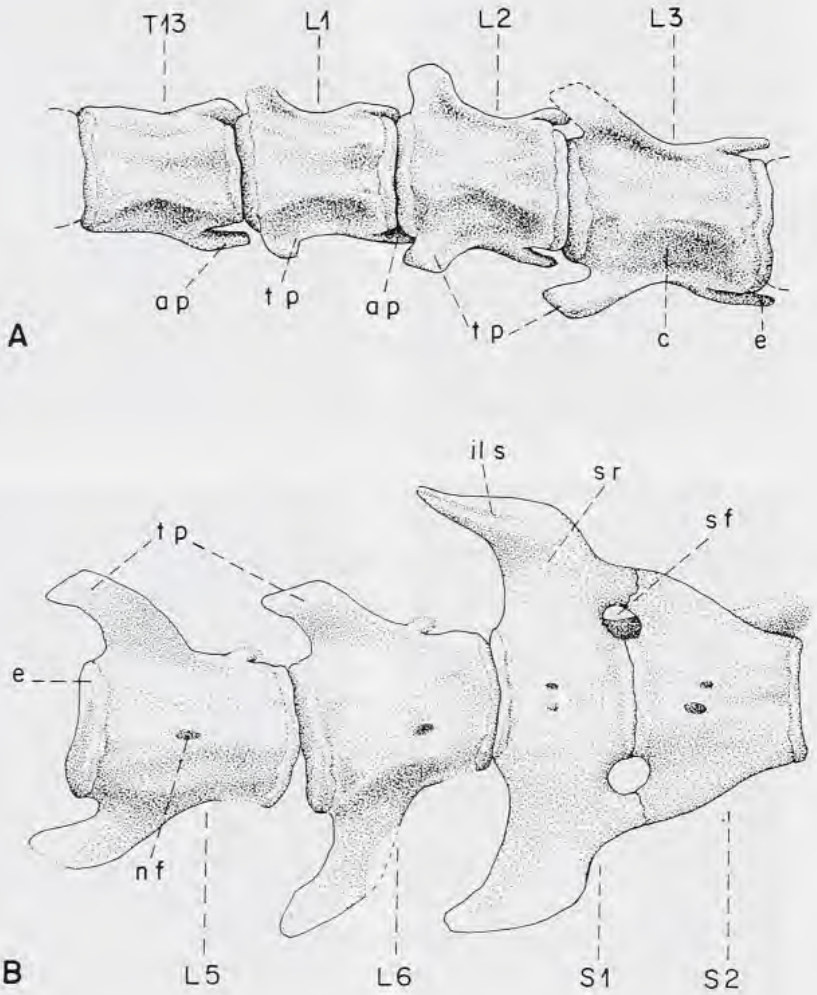


FIG. 32. — *Pucadelphys andinus*. 6106, thoracic, lumbar and sacral vertebrae: A, T13 and L1-3 (ventral face); B, L5-6, and Sl-2 (ventral face). X 5. All drawn as preserved. Abbreviations: **ap**, anapophysis; **c**, centrum; **e**, epiphysis; **il s**, iliac surface; **n f**, nutrient foramen; **s f**, sacral foramen; **s r**, sacral rib; **t p**, transverse process.

FIG. 32. — Pucadelphys andinus. *6106, vertèbres thoraciques, lombaires et sacrées: A, T13 et L1-3 (face ventrale); B, L5-6, et S1-2 (face ventrale). X 5. Dessin en l'état de conservation. Abréviations:* **ap**, *anapophyse;* **c**, *centrum;* **e**, *épiphyse;* **il s**, *surface iliaque;* **n f**, *foramen nourricier;* **s f**, *foramen sacré;* **s r**, *côte sacrée;* **t p**, *processus transverse.*

Source : MNHN, Paris

1880-1020, respectively); special emphasis was laid on *Metachirus* because this taxon is one of, if not the, most primitive extant member of this group (REIG *et al.*,1987). For these comparisons, the works by COUES (1872), SLIPJER (1946) and TATE (1933) were also used.

The first point to be noted is the vertebral formula: *Pucadelphys* has 7 cervicals, 13 thoracics, 6 lumbars, 2 sacrals and ± 30 caudals, which is similar to that of many living didelphids (*e.g. Didelphis, Metachirus, Philander*).

Atlas. — No atlas is preserved in *Henkelotherium*. Sutural linkage of the ossified intercentrum with the atlantal arch, as suggested in the above description of *Pucadelphys*, was also observed in *Barunlestes*, but not *Asioryctes* or *Eozostrodon*. A persisting suture between these two components makes the atlas of *Pucadelphys* less derived than in *Metachirus, Monodelphis* and *Didelphis*, where synostosis is complete. The presence of a fully enclosed transverse canal (though very narrow) is recorded in *Barunlestes* and considered as a derived state; this canal is not present in *Asioryctes, Didelphis, Monodelphis* or *Metachirus* (which means that the arteria vertebralis ran in a groove at the base of the transverse process); it thus seems doubtful that the tiny canal mentioned in *Pucadelphys* 6110 (Fig. 28, t c?) is homologous with the transverse canal, since the arterial sulcus is clearly visible at the base of the transverse apophysis; besides, a tiny canal similar to that in *Pucadelphys* is recorded in *Caenolestes* by OSGOOD (1921), who does not consider it as homologous to the transverse canal. On the other hand, the non closure of the canal for cranial nerve I as described in *Pucadelphys* is known only in three living marsupial genera (*i.e. Perameles, Marmosa* and *Monodelphis*). Other similarities with *Monodelphis* and *Metachirus* include the shallowness of the concavity of the axial facet and the shape of the transverse process.

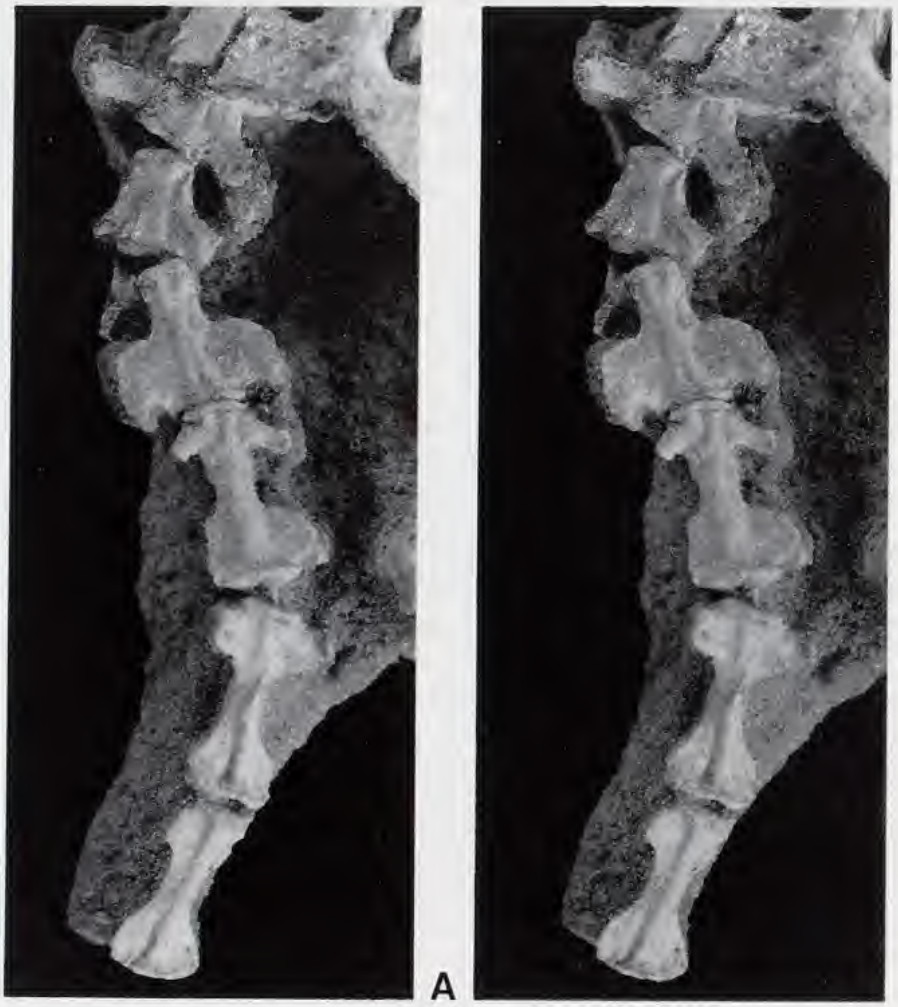
In conclusion, only one character of the atlas of *Pucadelphys* (persisting suture between ossified intercentrum and atlantal arch) is more primitive than in the atlas of the living non-specialized didelphids.

Axis. — No axis is preserved in *Henkelotherium*. The large intervertebral space (between atlas and axis) observed in *Pucadelphys* was also recorded in *Eozostrodon* and, based on the regular anterior concavity of the axis, was probably present in *Asioryctes* and *Barunlestes*. Among the examined didelphids, this space is longest in *Didelphis*, where the axis is very specialized anteriorly (*i.e.* the spinous process is very deep with a ventrally protracted anteroventral edge).

The suture visible between the atlantal and axial components of the axis body (less accentuated in the adult 6105 than in the subadult 6110) is typical of primitive mammals as well as living adult marsupials: it is discernible in *Metachirus* (but only faintly visible in *Perameles, Monodelphis* and *Didelphis)* and is also recorded in *Zalambdalestes* and *Asioryctes*. The axial part is shorter than the atlantal part (dens excluded) in these last two genera; it is longer in *Metachirus, Monodelphis, Perameles* and *Didelphis*, as in *Pucadelphys*.

The axis spine of *Pucadelphys* is not as specialized as in *Asioryctes* or *Zalambdalestes*. It is also not as specialized as in *Didelphis* or *Perameles*, but is very similar to that of *Metachirus* and *Monodelphis*; as already mentioned, the anterior border of the axial arch in *Pucadelphys* is indeed more similar in shape and orientation to that of *Metachirus* than to that of *Didelphis*, where

Source : MNHN, Paris



Source : MNHN, Paris

it is more sharply inclined ventrally. As for the posterior border, it slightly contacts the arch of CV3 as in *Metachirus* and *Monodelphis*, but not *Philander*.

The two roots of the transverse process, separated in *Pucadelphys*, are united in the living marsupials as well as in *Zalambdalestes*; thus, the absence of a transverse canal in *Pucadelphys* represents the plesiomorphic state. Finally, an unfused axial rib may have been present in *Pucadelphys*: among living marsupials a freely articulating cervical rib is only reported in *Perameles* (GRASSÉ, 1967: 608), *Caenolestes* and *Phascogale* (OSGOOD, 1921).

In conclusion, the axis shows two characters (absence of transverse canal -only the sulcus is present-, unfused axial rib) less derived than in generalized living didelphids.

Cervicals 3-7. — The epiphyses of the cervical vertebral bodies are not distinct in *Henkelotherium* or *Eozostrodon*, but remain so in *Pucadelphys* (and in the examined marsupials except *Didelphis*). In contrast, the neural-centrum suture is open in *Henkelotherium* but not in *Pucadelphys*. The shape of the vertebral body of the latter is similar to that of *Metachirus*. The neural spines are rod-like in *Eozostrodon*, low in *Henkelotherium* and *Metachirus*, almost non existant in *Perameles*, *Monodelphis* and *Philander* (at least until CV5) but high in *Didelphis* where they synostose with each other (a specialization of that genus); they were reduced to tubercles in *Asioryctes* and zalambdalestids, and apparently low and separated in *Pucadelphys*.

An enclosed transverse canal is present in CV3-CV6 of *Pucadelphys*, but absent on CV7 as in zalambdalestids, *Metachirus*, some specimens of *Caenolestes* and several other marsupials (e.g. *Perameles)*; this again represents the plesiomorphic state. There were no cervical ribs other than axial in *Pucadelphys* (nor in *Henkelotherium*, but possibly some in *Eozostrodon*).

The presence of an inferior lamella on CV6 is typical of all therians known in that respect, including *Asioryctes* and *Barunlestes*; the situation is not known in *Henkelotherium*.

In conclusion, the cervical vertebrae in *Pucadelphys* resemble those of living generalized didelphids.

In summary, primitive characters of the cervical vertebrae of *Pucadelphys* (i.e. absence of a transverse canal on atlas, axis and CV7, possible axial rib, shape of the axis arch) are not collectively found in any of the living didelphids examined.

Thoracic vertebrae. — In *Henkelotherium* the number of thoracics and even presacrals is not known, and no certain thoracic vertebra is preserved.

The number of thoracics in *Pucadelphys* (13) is the same as in living didelphids and *Perameles*. T8-T9 are transitional vertebrae in *Pucadelphys* (Fig. 30C) and *Monodelphis*, T7-8 in *Didelphis* (Fig. 30A), T9 in *Philander* and T9-10 in *Metachirus* (Fig. 30B).

FIG. 33. — *Pucadelphys andinus*. Stereophotos. A, 6106, vertebrae C4 to C9, ventral view. X 3; B, 6105, left partial pes, dorsal view. X 3.

FIG. 33. — Pucadelphys andinus. *Stéréophotos. A, 6106, vertèbres C4-C9, vue ventrale. X 3; B, 6105, pied gauche partiel, vue dorsale. X 3.*

Source : MNHN, Paris

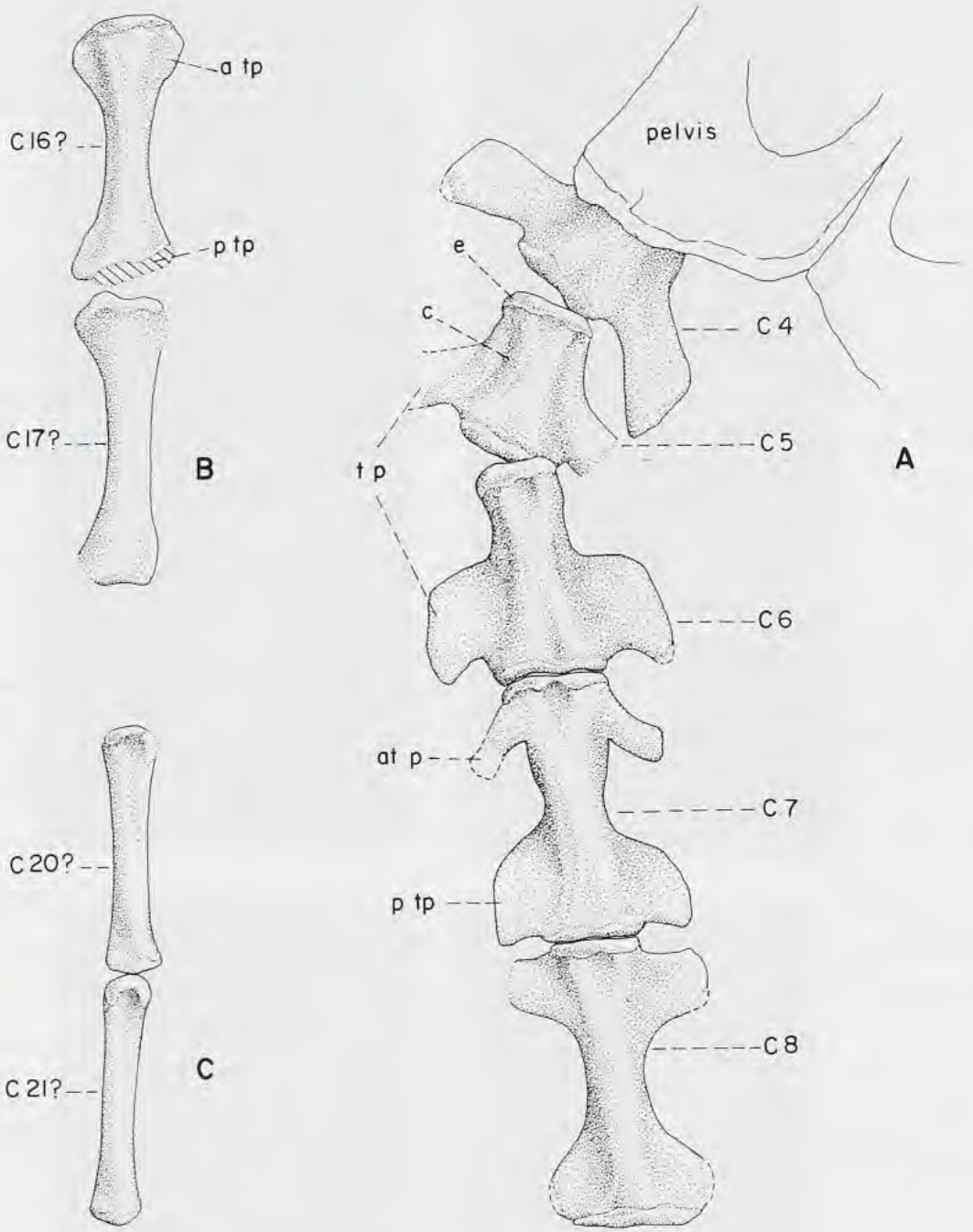


FIG. 34. — *Pucadelphys andinus*. Caudal vertebrae: A, 6106, C4 to 8, ventral face; B, 6110, C17?, C18?, C20? and C21?, ventral face. X 5. All drawn as preserved. Abbreviations: **at p**, anterior transverse process; **e**, epiphysis; **c**, centrum; **t p**, transverse process; **p tp**, posterior transverse process.

FIG. 34. — Pucadelphys andinus. *Vertèbres caudales: A, 6106, C4-C8, face ventrale; B, 6110, C17?, C18?, C20?, et C21?, face ventrale. X 5. Dessins en l'état de conservation. Abréviations;* **at p**, *processus transverse antérieur;* **e**, *épiphyse;* **c**, *centrum;* **t p**; *processus transverse;* **t p**, *processus transverse postérieur.*

Source : MNHN, Paris

In *Asioryctes* (only the first thoracic is preserved) and *Barunlestes* (the last three preserved), the transverse processes are short; there is no spine, only a tubercle; the vertebral body is wider than long; and accessory processes (meta- and anapophyses) are also present.

In *Didelphis, Perameles* and *Metachirus*, the thoracic spines, longer in the anterior part of the series than in *Pucadelphys*, become short and stouter posteriorly; in *Monodelphis* and *Philander*, they are short and inclined more and more posteriorly, while in *Didelphis* they contact each other on the posterior vertebrae, a specialized state relative to that of the other genera. In *Pucadelphys*, there is no evidence of an anticlinal spine, no more than in living didelphids, but in *Perameles* the spinal orientation reverses at T11. Finally, in *Pucadelphys, Metachirus* and *Perameles*, the epiphyses are distinct, whereas they are hardly so in *Didelphis* or *Monodelphis*.

In conclusion, the thoracic series in *Pucadelphys*, though not completely preserved, is comparable to that of the living didelphids.

Lumbar vertebrae. — The number of lumbars is not known for certain in *Henkelotherium*, but is estimated to be at least six; there were possibly seven in *Barunlestes*, and there are six in living didelphids as in *Pucadelphys*. In *Pucadelphys, Metachirus, Monodelphis* and *Perameles*, as in *Barunlestes*, the lumbars show a lengthening of the body more posteriorly in the series than in *Henkelotherium, Philander* or *Didelphis*. The epiphyses are distinct in the latter genera, not by a suture, but by a thickening of the ends; they remain distinct by a suture in *Pucadelphys*, *Metachirus* and *Perameles*.

In *Pucadelphys*, the lumbar spinous processes are narrow, high and dorsally or anteriorly directed as in *Perameles*; in *Metachirus*, they are long, low and posteriorly oriented in the anterior lumbars, then they become higher, straight and finally slightly anteriorly directed; this arrangement is intermediate between that in *Pucadelphys* on the one hand, and that in *Didelphis* or *Philander* in the other, where they are all low and posteriorly directed except on L6; the same is true of *Monodelphis*, but the spines are even lower. The latter were long and low in *Barunlestes*, at least on L3. In *Henkelotherium* the spinous processes are not preserved.

Accessory processes are recorded on the lumbars of *Eozostrodon*; in *Henkelotherium* the anapophyses seem to be well developed; in *Metachirus* and *Pucadelphys* they are better developed than on the thoracics. They remain discrete in *Monodelphis*, where only metapophyses are developed, but they are stout in *Didelphis*. Their development seems to be related to a reduction of lateral flexion.

The short transverse processes of the lumbars of *Henkelotherium* do not seem to show an elongation towards the sacrum. They are also short in *Barunlestes* "as in *Didelphis*" (KIELAN-JAWOROWSKA, 1977); those of *Metachirus* and *Pucadelphys* form a very similar gradual series, being anterolaterally directed (as in *Perameles*), while those of *Philander* and *Monodelphis* are more discrete and those of *Didelphis* are more robust and form a more rigid ensemble.

In conclusion, the lumbar vertebrae of *Pucadelphys* form a rather specialized series (within didelphids at least), with a gradual lengthening of the body and transverse processes, and long neural spines anteriorly directed; this situation is comparable to that of *Perameles*.

Source : MNHN, Paris

Sacral vertebrae. — The sacrum is relatively much longer in *Barunlestes* than in *Pucadelphys*, due principally to elongation of S2. But in both genera, it is made of two vertebrae and there is only one fulcral vertebra. According to KIELAN-JAWOROWSKA (1978) this situation is primitive for Eutherians (the mean number of sacral vertebrae being 3). However, Lessertisseur & Saban (*in* GRASSÉ, 1967: 624) state: "le nombre total de vertèbres soudées en un sacrum est variable et ne permet guère d'envisager une ligne claire d'évolution". Besides, *Henkelotherium* has two true sacrals (with two robust sacral ribs), *Eozostrodon* two to three; in addition, cynodonts commonly had four to five (JENKINS, 1971), the Early Cretaceous triconodont *Gobiconodon* probably had three (JENKINS & SCHAFF, 1988) and monotremes do have three. This would seem to contradict KIELAN-JAWOROWSKA's statement. Among didelphids, the sacrum is made of two vertebrae; but whereas the two are almost equally apposed to the ilium in *Monodelphis* and *Didelphis*, there is only one and a half in *Philander* and only one in *Metachirus* (which incidentally covers less than 50% of the auricular surface of the ilium as opposed to more than 50% in *Pucadelphys*); moreover in *Metachirus*, S2, which has even a smaller contact with S1 than in *Pucadelphys*, has short transverse processes, shorter even than those of C1: clearly, in this taxon considered as primitive on other grounds, there is practically no differenciation of S2 towards a sacral status. But *Perameles*, which shows numerous specializations in that area, has the same sacral structure as *Metachirus* and *Pucadelphys*, with an even smaller auricular surface.

To conclude, if our interpretation of the lumbar vertebrae of *Pucadelphys* as derived is correct, it would seem coherent to consider its configuration of the sacrum as also derived, at least within didelphids.

Caudal vertebrae. — Comparison of the four distal caudals of 6110 with *Metachirus* indicates that they apparently correspond to C16? + C17?, and C20? + C21?. Assuming that the subsequent caudals were similar to those of the living didelphids (see below), the number of caudals for *Pucadelphys* is estimated to be about 30. The number in some living didelphids is as follows: *Monodelphis*, 18?; *Didelphis*, 26 to 29; *Chironectes*, 29 (FLOWER, 1885); *Philander*, 32; and *Metachirus*, 32. Also, *Pucadelphys* resembles *Monodelphis* and *Didelphis* in having 5 anterior caudals, a transitional C6, and the posterior caudals begin with C7; in *Metachirus* C5 is transitional while in *Philander* it is C4.

In *Didelphis*, the caudal vertebrae have specializations associated with a prehensile tail (KRAUSE & JENKINS, 1983: 242): e.g. tail long, commonly twice or more the length of the precaudal vertebral column; a median sulcus for abductor muscles and tendons crosses ventrally all the vertebrae, zygapophyses are more vertical, transverse processes are broad and robust for muscle attachments and present even in most distal caudals; moreover, haemal apophyses, that enclose abductor tendons and muscles, are large and developed along nearly entire length of tail; finally, sacral spinous processes are relatively well developed, commonly subequal to the height of the spinous processes of posterior lumbar vertebrae. No such specializations except high sacral spinous processes and a very slight ventral sulcus on caudals exist in *Philander* and *Metachirus*, haemal apophyses in *Monodelphis*; none of them were found in *Pucadelphys*. The caudal vertebrae of *Henkelotherium* also show prehensile specializations: haemapophyses, ventral sulcus, and mostly considerable elongation from C6.

Source : MNHN, Paris

The "evolution" of the caudal transverse processes observed along the tail is different in the examined didelphids: in *Didelphis* and *Monodelphis* the long transverse lamina divides into an anterior and a posterior component persisting together for a distance; in *Metachirus* the wide transverse process also divides, but the posterior component practically disappears on the vertebra following this division; in *Pucadelphys*, the situation is more complex than in this genus (see p. 109). As stated above, the transitional vertebra is C6 in *Pucadelphys, Didelphis, Monodelphis* and *Caenolestes*, and C5 in *Metachirus*.

Spinous processes are totally absent on the caudals of *Caenolestes* and *Monodelphis*, very faint in *Metachirus* and *Didelphis*, high on anterior caudals in *Perameles*, while rather low in *Pucadelphys*.

In conclusion, there is no indication that the tail was prehensile in *Pucadelphys*.

Appendicular Skeleton.

Shoulder Girdle

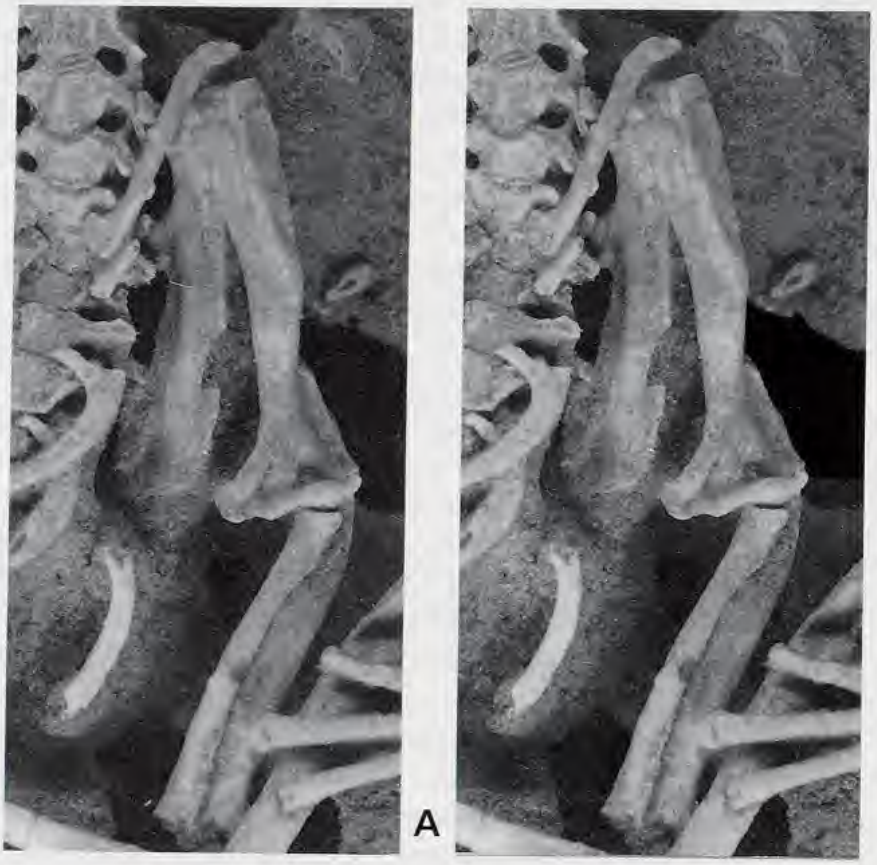
Scapula (Figs 24B, 35B, 36 and 38A; Table 7). — Four elements: 6105, left, external and partial internal views; 6106, partial right, internal and external views - distal extremity of left, internal view; 6110, distal fragment of left, internal view; 6111, proximal fragment of left, external view.

Notable features are the straightness of the posterior border (Fig. 36, pb), the relative anteroposterior narrowness of the scapular plate (s p), the slight anteroposterior convexity of the internal face along the posterior border, the anteromedial protrusion of the large coracoid process (c), and the depth of the supracoracoid incisure (s i). The plate itself is very thin and the suprascapular border (s b) is not thickened. The spine (s), for which we have only partial views (the best being on 6105), is very thin, relatively high and probably deflected; it decreases in height proximally. The acromion (a) (as preserved only on 6106, right) is a thin triangular (apex directed posteriorly) plate-like process, set perpendicular on the anterior part of the spine and parallel to the scapular blade. Its anterior edge extends slightly beyond, but parallels, that of the glenoid cavity (g c); its anterior-most projection lies nearly dorsal to the tuber scapulae (t s). The supraspinous fossa (s f) seems to have been slightly wider than the infraspinous fossa (i f) (testifying to a robust supraspinous muscle which itself contributes to a good shoulder mobility (Jenkins & Weijs, 1979: 408). The glenoid cavity is ovoid in shape, very shallow, and the tuber scapulae high but not prominent (for insertion of the coraco-humeral ligament). The margin of the glenoid fossa is only slightly thickened. What may be the scapulocoracoid suture is visible only in 6106 (left).

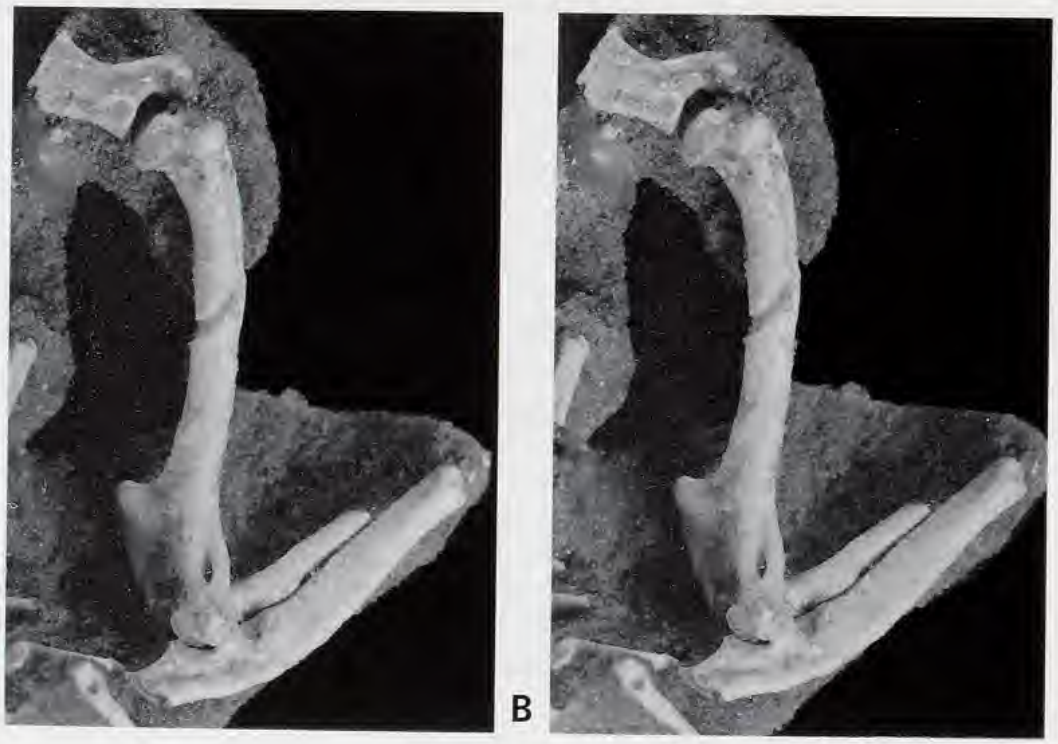
Clavicle (Figs 25B, 26B, 35A, 37A and 38; Table 8). — Three elements: 6105, nearly complete left, anterior view - sternal extremity of right, posterior view; 6110, almost complete right, posterior view - incomplete left, anterior and dorsal views.

The clavicle has the form of a very elongate S. The scapular extremity (Fig. 37, sc e) is slightly oblong and was probably thickened, but it is flattened as preserved; the sternal extremity

Source : MNHN, Paris



A



B

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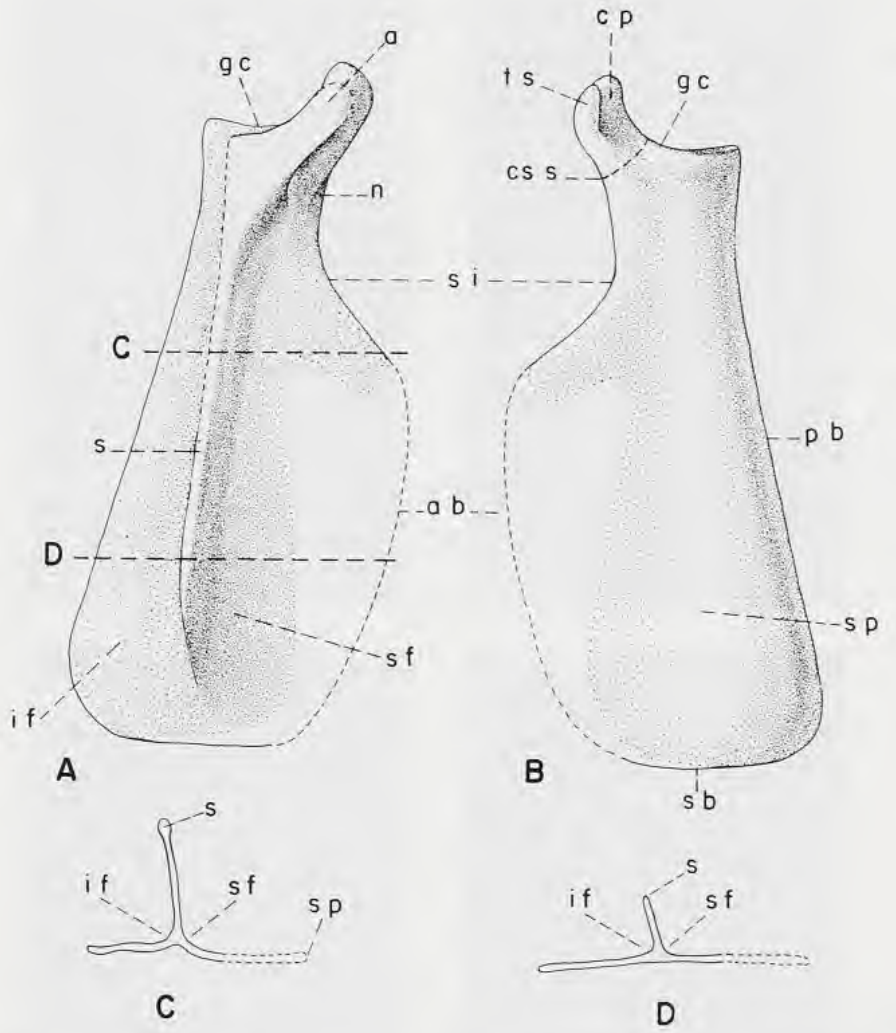


FIG. 36. — *Pucadelphys andinus*. Left scapula, reconstructed (6105 and 6106 combined): A, external face; B, internal face; C, anterior transverse section; D, posterior transverse section, X 5. Abbreviations: **a**, acromion; **a b**, anterior border; **c p**, coracoid process; **cs s**, coraco-scapular suture; **g c**, glenoid cavity; **i f**, infraspinous fossa; **n**, neck; **p b**, posterior border; **s**, spine; **s b**, suprascapular border; **s f**, supraspinous fossa; **s i**, suprascapular incisure; **s p**, scapular plate; **t s**, tuber scapulae.

FIG. 36. — Pucadelphys andinus. *Omoplate gauche reconstituée (basée sur 6105 et 6106): A, face externe; B, face interne; C, section transversale antérieure; D, section transversale postérieure. X 5. Abréviations:* **a**, *acromion;* **a b**, *bord antérieur:* **c p**, *processus coracoïdien;* **cs s**, *suture coraco-scapulaire;* **g c**, *cavité glénoïde;* **i f**, *fosse sous-épineuse;* **n**, *col;* **p b**, *bord postérieur;* **s**, *épine;* **s b**, *bord supra-scapulaire;* **s f**, *fosse sus-épineuse;* **s i**, *incisure suprascapulaire;* **s p**, *lame scapulaire;* **t s**, *tuber scapulae.*

FIG. 35. — *Pucadelphys andinus*. Stereophotos. A, 6105, left clavicle, scapula, humerus, ulna and radius, ventroposterior view. X 3; B, 6106, distal extremity of left scapula, humerus, ulna and radius, posterolateral view. X 3.

FIG. 35. — Pucadelphys andinus. *Stéréophotos. A, 6105, clavicule gauche, omoplate, humérus, cubitus et radius, vue ventro-postérieure. X 3; B, 6106, extrémité distale de l'omoplate gauche, humérus, cubitus et radius, vue postéro-latérale. X 3.*

Source : MNHN, Paris

(st e) is much flatter and expanded, concave anteriorly (for the omosternal cartilage linking it to the interclavicle) with a raised and thickened posterior border; it is situated at a right angle relative to the shaft; its posterior face is relatively flat. The anterior face of the shaft shows a spiral-like transverse convexity, while the posterior face is flatter.

Interclavicle (Figs 25B and 37B; Table 9). — Preserved only in 6105, very slightly distorted, ventral and partial dorsal views.

The interclavicle is well ossified and relatively long; the anterior process (which supports anteriorly the clavicle) and the posterior process (which supports the first rib laterally) are only slightly unequal in breadth, but the anterior part is shorter than the posterior one. Ventrally it bears a long and high keel which heightens distally, where the bone is as high as it is wide. The short triangular arms face laterally and terminate with a "costal tubercle" (Fig. 37, c t). A broad anteroposterior sulcus occurs at the base of the arms between the median ridge (m r) and costal tubercle. Dorsally the bone seems to have been slightly concave.

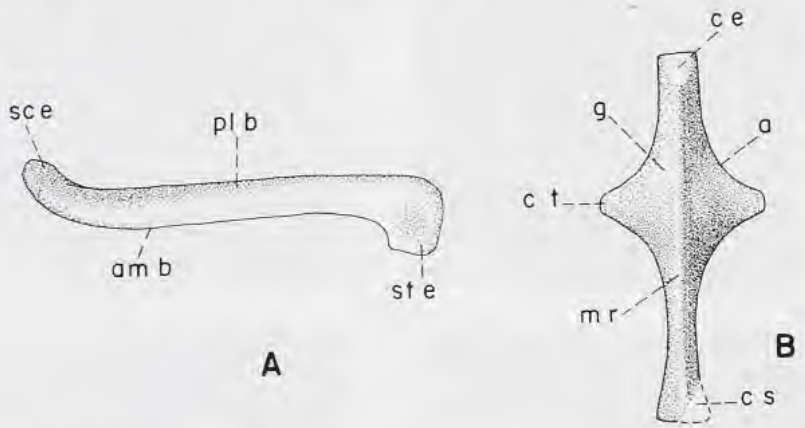


FIG. 37. — *Pucadelphys andinus*. 6105: A, left clavicle and B, interclavicle, ventral face. X 5. Drawn as preserved. Abbreviations: **a**, transverse arm; **am b**, anteromesial border; **c e**, cephalic extremity; **c s**, caudal surface; **c t**, costal tubercle; **g**, groove; **m r**, median ridge; **pl b**, posterolateral border; **sc e**, scapular extremity; **st e**, sternal extremity.

*FIG. 37. — Pucadelphys andinus. 6105: A, clavicule gauche et B, interclavicule, face ventrale. X 5. Dessins en l'état de préservation. Abréviations: **a**; branche transversale; **am b**, bord antéro-mésial; **c e**; extrémité céphalique; **c s**, surface caudale; **c t**, tubercule costal; **g**, sillon; **m r**, côte médiane; **pl b**, bord postéro-latéral; **sc e**, extrémité scapulaire; **st e**, extrémité sternale.*

FORELIMB

Humerus (Figs 35, 38 and 39; Table 10). — Six elements: 6105, nearly complete left, anterior view - distal half of right, all views; 6106, most of right diaphysis, anterior view - complete left, posterointernal view; 6110, nearly complete right, posterior view - nearly complete left, internal view; 6111, distal half of left, posterointernal view - a small fragment of the distal end of the right.

The humerus is stout. The head (Fig. 39, h) covers about 50% of the width of the proximal end, and extends only slightly beyond the level of the tuberosities; it is transversely narrow and

Source : MNHN, Paris

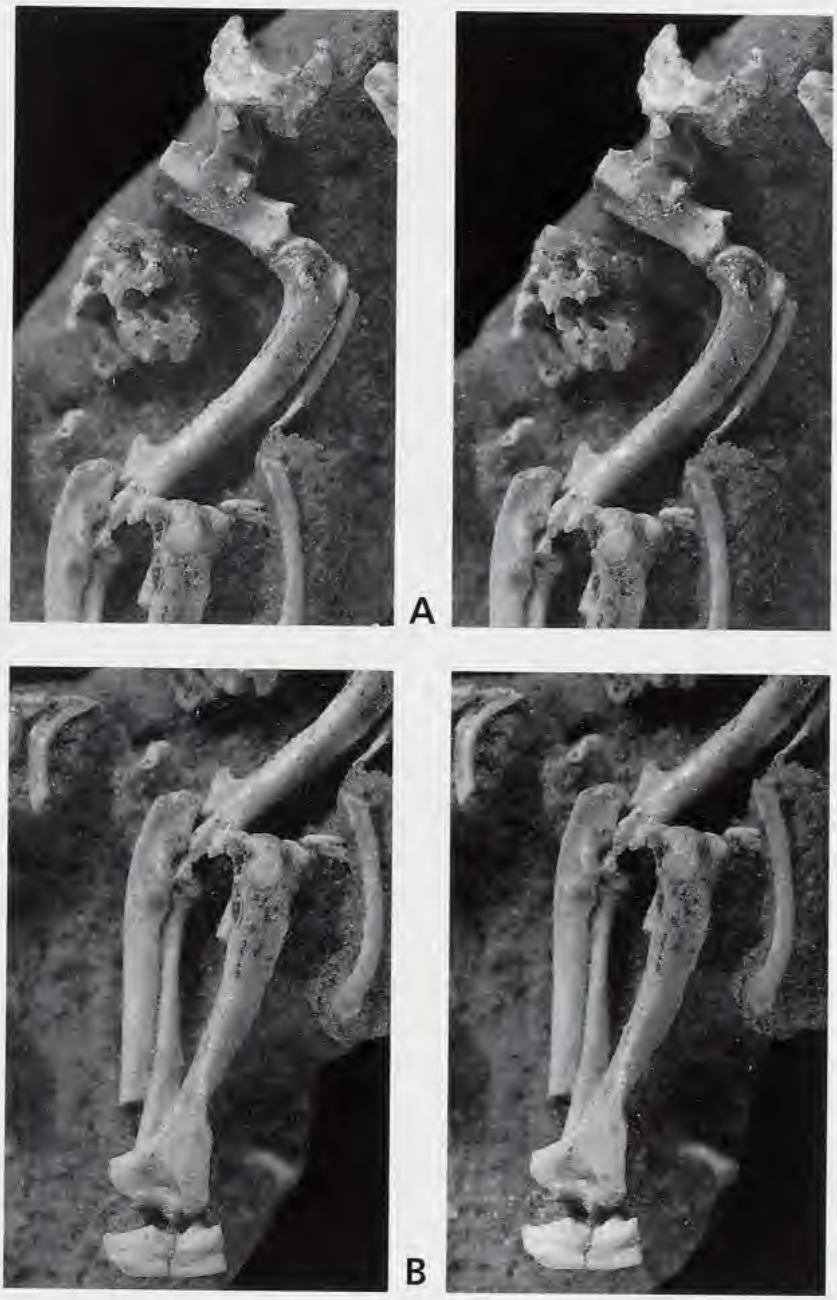


FIG. 38. — *Pucadelphys andinus*. Stereophotos. A, 6110, axis, left lateral view; fragments of left scapula and humerus, internal view; left clavicle, anterior view. X3; B, 6110, right humerus, posterior view, left ulna and radius, internal view; left clavicle, posterior view, X 3.

FIG. 38. — Pucadelphys andinus. *Stéréophotos. A, 6110, axis, vue latérale gauche; fragments d'omoplate gauche et d'humérus, vue interne; clavicule gauche, vue antérieure. X 3; B, 6110, humérus droit, vue postérieure; cubitus et radius gauches, vue interne; clavicule gauche, vue postérieure. X 3.*

Source : MNHN, Paris

curves sharply posteroventrally. The greater tuberosity (g t) is subequal in breadth, but is overall larger, than the lesser tuberosity (l t); it is separated from the head by a slight sulcus, and grades distally into a long deltopectoral crest (dp c) which extends half the length of the diaphysis. The large deltopectoral surface is triangular (apex points distally), planar, and somewhat turned down internally; it bears only small rugosities. The lesser or internal tuberosity is not sharply demarcated from the head (only a narrow sulcus is visible on the left side of 6106). A wide and deep bicipital groove (b g) separates the two tuberosities anteriorly and continues distally between the deltoid

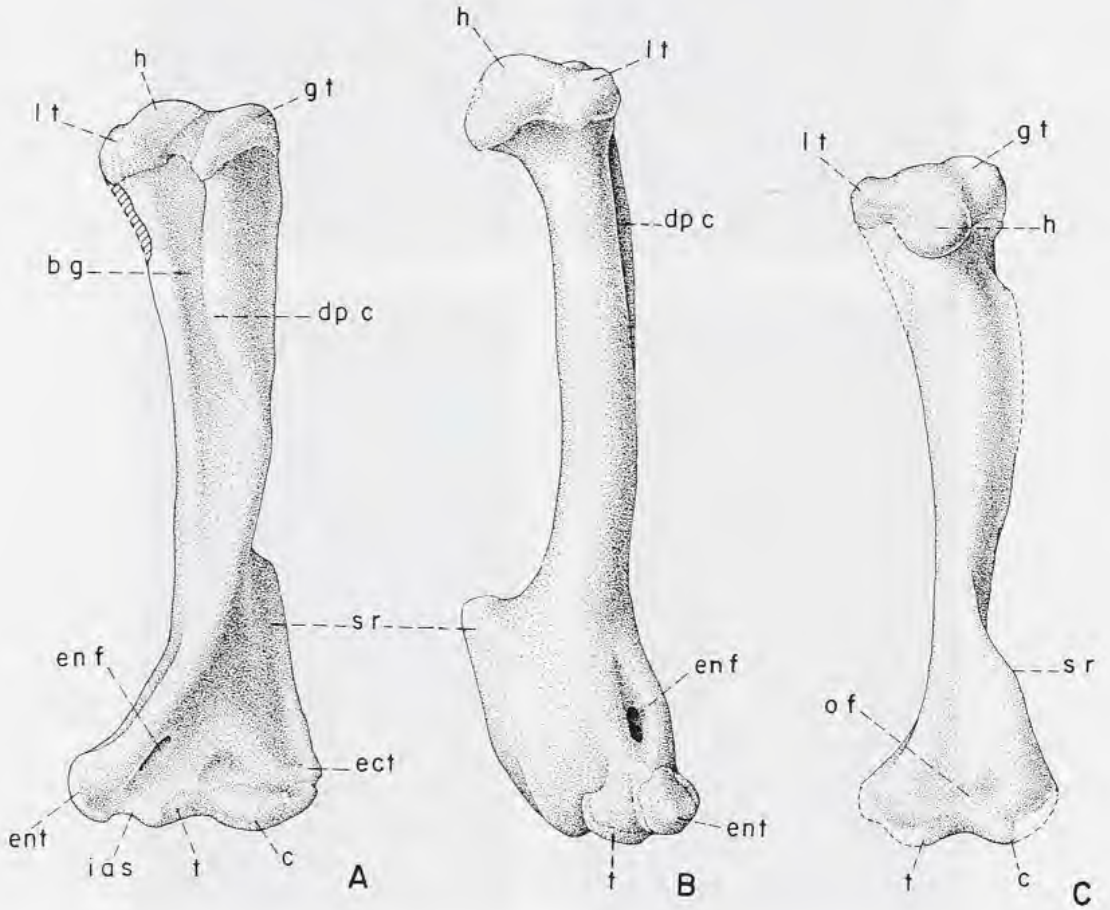


FIG. 39. — *Pucadelphys andinus*. Humerus: A, 6105, left, anterior face; B, 6106, left, posteromesial face; C, 6110, right, posterior face. X 5. All drawn as preserved. Abbreviations: **b g**, bicipital groove; **c**, capitulum; **dp c**, deltopectoral crest; **ect**, ectepicondyle; **ent**, entepicondyle; **en f**, entepicondylar foramen; **g t**, greater tuberosity; **h**, head; **i a s**, internal articular sulcus; **l t**, lesser tuberosity; **o f**, olecranon fossa; **s r**, supinator ridge; **t**, trochlea.

FIG. 39. — Pucadelphys andinus. *Humérus: A, 6105, gauche, face antérieure; B, 6106, gauche, face postéro-mésiale; C, 6110, droit, face postérieure. X 5. Dessins en l'état de conservation. Abréviations:* ***b g****, sillon bicipital;* ***c****, capitulum;* ***dp c****, crête delto-pectorale;* ***ect****, ectépicondyle;* ***ent****, entépicondyle;* ***en f****, foramen entépicondylien;* ***g t****, grande tuberosité;* ***h****, tête;* ***ias****, sillon articulaire interne;* ***l t****, petite tubérosité;* ***o f****, fosse olécranienne;* ***s r****, crête du supinateur;* ***t****, trochlée.*

Source : MNHN, Paris

crest and the posteroexternal border of the bone. Distal to the deltopectoral crest, the diaphysis is narrow, subcylindrical in cross-section; but the bone rapidly flattens anteroposteriorly and flares transversely; at that level, it is limited externally by a broad and thin supinator ridge (s r) that extends along about 30% of the diaphysis. Internally this expanded part is limited by the entepicondylar "crest" which consists of two ridges that border a pronounced sulcus, itself perforated by an elliptical entepicondylar foramen (en f); the anterointernal ridge ascends obliquely toward the deltopectoral crest. The suture between the proximal epiphysis and the diaphysis remains distinct in adults.

The distal end is transversely wide, but the articular surfaces are low and occupy only a narrow part of this width. The small ectepicondyle (ect) is not thickened anteroposteriorly; the entepicondyle (ent) is ovoid, slightly convex, and protrudes internally. External to it is a broad sulcus, sharply delimited posteriorly on its external side, less sharply anteriorly, and obliquely oriented (this is the internal articular sulcus of OSGOOD (1921), which in *Caenolestes* receives the inner upper lip of the sigmoid cavity of the ulna). The capitulum (c) is wide anteriorly; posteriorly it is reduced to a crest reaching the level of the base of the entepicondylar foramen. Anteriorly the trochlea (t) and capitulum grade into one another without delimitation; posteriorly and above the capitulum, the bone is depressed by a deep and short fossa which receives the olecranon during flexion of the forearm (o f). The measurements effected on the humerus of 6110 according to the method proposed by KIELAN-JAWOROWSKA & GAMBARYAN (1994) indicate that there was practically no twisting of the bone.

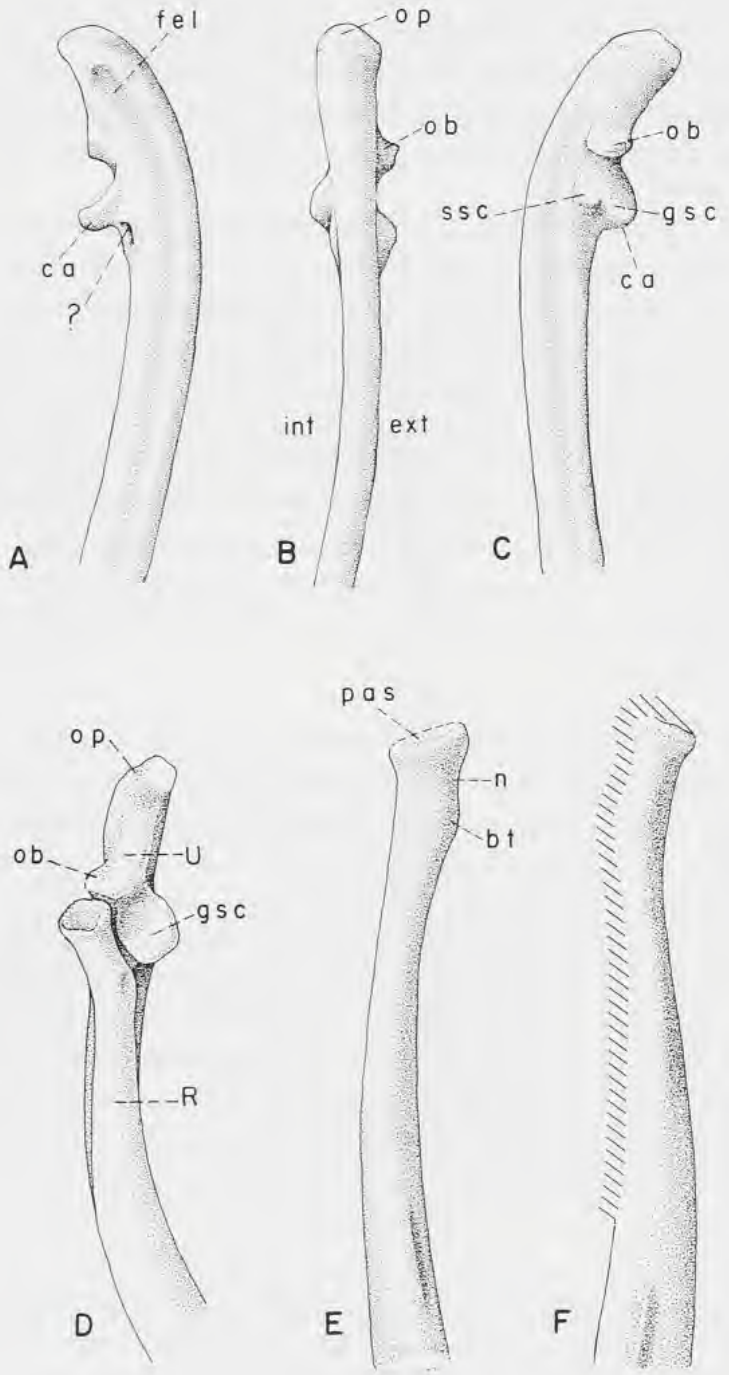
Ulna (Figs 35, 38B, 40A-D and 45C; Table 11). — Six elements: 6105, left, complete except for distal epiphyses, anteroexternal view - isolated proximal half of right, internal, external and posterior views; 6106, proximal half of left, internal view (olecranon incomplete); 6110, left, internal view - right proximal part, external view; 6111, median fragment of left diaphysis - isolated proximal half of right, anterointernal view.

In length, the ulna is equal to or slightly greater than the humerus. It is wider than the radius, hence stout. The olecranon process is long, with a convex upper border (6111 right); it is slightly inclined internally; there is no terminal tubercle. The anterior margin of the olecranon appears to be slightly concave. Its internal face is depressed by a longitudinal sulcus, while its external face is practically flat. The "beak" of the olecranon is directed externally, with no internal projection.

The greater sigmoid cavity (g s c) is narrow, high, oblique dorsoventrally and externointernally, convex transversely on the internal part for the humerus, and flat on the external part, also apparently for the humerus. The lesser sigmoid cavity (s s c) for the radius is apparently small and only slightly excavated. There is a well developed coronoid apophysis (c a), but there is no internal coronoid tubercle; this apophysis is strongly protruding internally, anteriorly underlain by a depression with an orifice, and limited laterally by a strong ridge. The diaphysis is very compressed laterally so as to form a ridge posteriorly; distally it becomes more ovoid, slightly arched and slightly narrower. No distal extremity is preserved; the most complete specimen (6105) did not have the distal epiphysis fused, and it was lost during fossilization.

Radius (Figs 35, 38B, 40D-F and 45C; Table 12). — 6105, left, complete except for distal

Source : MNHN, Paris



Source : MNHN, Paris

epiphysis, anteroexternal view - isolated, proximal half of right, anterior, external and internal views; 6106, left proximal third, internal view; 6110, left, internal view; 6111, fragment of left diaphysis - isolated proximal half of right, anterointernal view.

The anteroposterior curvature of the bone is gentle, the lateral one is more pronounced distally. The proximal articular surface (Fig. 40, p a s) is ovoid and compressed with a transverse long axis, and noticeably concave. Under the thickened proximal border, there follows a neck (n), itself immediately followed by a strong bicipital tuberosity (b t), rather highly situated. The anterior face of the bone is convex proximally, becomes flat distally, the anterior ridge quickly disappearing; the external face, wide proximally, becomes more convex distally, where a median sulcus is discernible, presumably for the ulnar crest; the internal face narrows to a ridge distally. The diaphysis is triangular in cross-section at mid-length. No distal extremity is preserved.

In each case, the ulna and radius are, as preserved, in contact along nearly their entire length: only under the bicipital tuberosity is there a very narrow interosseous space. This testifies to a very limited capacity of rotation. Proximally the bones are situated anteroposteriorly relative to each other, but soon torsion brings the radius in an internal position relative to the ulna.

Manus. — Nothing is unquestionably preserved of the hand, but see cautionary remarks under pes (p. 139).

Discussion

Scapula. — In *Megazostrodon*, there is no distinct supraspinous fossa. In *Henkelotherium*, the scapula remains more primitive than in *Pucadelphys* with a massive coracoid component, but the supraspinous fossa is said to cover almost two-thirds of the external surface.

No scapula is preserved in *Asioryctes*. In *Barunlestes*, where the ventral part is preserved, the extensive tuber scapulae and the coracoid process were developed in a way more reminiscent of metatherians than of modern claviculate eutherians. In *Pucadelphys*, the tuber scapulae is smaller than the coracoid process, as in *Metachirus*. In *Barunlestes*, the spine starts at about the same level as in *Pucadelphys*, that is, slightly higher than in *Didelphis*. In the latter, the two fossae are subequal (as in *Perameles*), the spine is thicker than in *Pucadelphys*, the posterior border more convex, the glenoid cavity flatter and more complex, and the internal face regularly concave; there is no overhang of the coracoid process, and the plate itself is relatively thicker.

In *Philander*, the infraspinous fossa remains very slightly larger than the supraspinous

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Fig. 40. — *Pucadelphys andinus*. A-C, 6105, proximal part of right ulna: A, internal face; B, posterior face; C, external face. D, isolated, proximal end of articulated right ulna and radius, anterior view; E-F, proximal end of left radius: E, 6105, internal face; F, 6110, anteroexternal face. X 5. All drawn as preserved. Abbreviations: **b t**, bicipital tuberosity; **c a**, coronoid apophysis; **ext**, external; **f e l**, fossa for exterior ligament; **g s c**, greater sigmoid cavity; **int**, internal; **n**, neck; **o b**, olecranon beak; **o p**, olecranon process; **p a s**, proximal articular surface; **R**, radius; **s s c**, lesser sigmoid cavity; **U**, ulna.

Fig. 40. — Pucadelphys andinus. *A-C, 6105, partie proximale du cubitus droit: A, face interne; B, face postérieure; C, face externe; D, spécimen isolé, extrémité proximale du cubitus et du radius en articulation, vue antérieure; E-F, extrémité proximale du radius gauche: E, 6105, face interne; F, 6110, face antéro-externe. X 5. Dessins en l'état de conservation. Abréviations:* **b t**, *tubérosité bicipitale;* **c a**, *apophyse coronoïde;* **ext**, *externe;* **f e l**, *fosse pour le ligament externe;* **g s c**, *grande cavité sigmoïde;* **int**, *interne;* **n**, *col;* **o b**, *bec de l'olécrane:* **o p**, *processus olécranien;* **p a s**, *surface articulaire proximale;* **R**, *radius;* **s s c**, *petite cavité sigmoïde;* **U**, *cubitus.*

Source : MNHN, Paris

fossa; otherwise the bone is comparable to that of *Metachirus;* but in the latter as in *Monodelphis*, it is the supraspinous fossa which is slightly larger than the infraspinous, the spine is very thin, the posterior border straight, and the acromion not thickened, all character states as in *Pucadelphys*. However, in *Metachirus* the tuber scapulae is lower, and the coracoid process less recurved internally than in the other two genera; the coracoscapular suture remains distinct, at least in the subadult specimen which we used for comparisons. Finally, the scapula of *Monodelphis* has a deflected spine as in *Pucadelphys*.

It thus appears that *Pucadelphys* has an unspecialized scapula, combining all primitive character states found isolated in living didelphids.

Clavicle. — The assignment of this bone to *Eozostrodon* is only tentative. The clavicle of *Henkelotherium*, which must have been quite long, is rounder than that of *Pucadelphys* and not widened sternally. No clavicle is preserved in the Mongolian eutherians.

The clavicle of *Didelphis* shows the same general features as that of *Pucadelphys* (but the torsion is more accentuated relative at least to the preserved state in *Pucadelphys*, which may be the result of some flattening during fossilization) and the interclavicular extremity more flattened; also the scapular extremity does not make an angle on the long axis; finally it is relatively shorter (1/2 of length of the scapula, compared to 2/3 in *Pucadelphys*).

In *Metachirus*, the clavicle is not as clearly S-shaped as in *Pucadelphys*, and there is no posterior spiral convexity; but the sternal extremity is hollowed ventrally with a raised medial border as in *Pucadelphys*. The clavicle of *Monodelphis* is more similar to that of *Pucadelphys*, but its sternal extremity, though less angled relative to the shaft, is relatively wider; the same is true of *Metachirus*. In *Perameles,* the clavicle is absent or rudimentary.

In conclusion, the clavicle of *Pucadelphys* is that of a typical non specialized didelphid.

Interclavicle. — The homologies of this bone have been widely disputed; it seems logical to consider it as homologous to the episternum of monotremes and to the "manubrium" of *Caenolestes* (Osgood, 1921). No interclavicle is known in Cretaceous therians, and, according to Krebs (1991), none was developed in *Henkelotherium*. As for *Eozostrodon*, the same remarks noted for the clavicle apply to the interclavicle.

In *Didelphis*, the interclavicle is shorter than in *Pucadelphys* and the arms divide it longitudinally into two equal parts; it is also more concave dorsally, and the ventral keel completely disappears distally. Similarly in *Perameles,* this keel becomes considerably lower distally. In *Metachirus* the bone is very similar to that of *Pucadelphys*. In *Monodelphis*, the anterior and posterior parts are also quite unequal as in the latter two genera, but there is practically no ventral keel.

Overall, the interclavicle of *Pucadelphys* is typically didelphid.

Humerus. — In *Henkelotherium,* the bone is long and robust; a peculiarity is a strongly marked muscular insertion on the mesial face of the shaft not found in *Pucadelphys*, which presumably would represent the derived state for this character: in *Eozostrodon* the bump is even more accentuated than in *Henkelotherium*. Also in the latter, the deltoid crest is robust but

Source : MNHN, Paris

relatively shorter (1/3 of the bone against 1/2 in *Pucadelphys*). The entepicondyle is prominent. Compared to *Barunlestes*, 6105 has a less curved diaphysis, the deltopectoral crest is more prominent; there is the same groove between both tuberosities. But most notable is the difference concerning the distal extremity, which is much wider in *Pucadelphys*; also the entepicondyle is better developed and there is no supratrochlear foramen; finally, the susepicondylian crest is lacking in *Barunlestes*, and the supinator ridge is not as wide and sharp.

In *Metachirus*, the bone is relatively more slender than in *Pucadelphys*, the deltopectoral surface is as smooth and long but not deflected as in *Pucadelphys*, and the supinator ridge is relatively shorter. There is no third distal articular surface; such a feature, described above in *Pucadelphys*, is mentioned by OSGOOD (1921) for *Caenolestes* as being exceptional for marsupials, and he considers it as more indicative of digging than cursorial habits. The humerus of *Didelphis* is more similar to that of *Pucadelphys* than to that of *Metachirus*: the proportions of the bone are slightly different and the head is relatively wider, but dorsally the latter does not extend beyond the tuberosities any more than in *Pucadelphys*; the deltopectoral ridge extends over half of the length of the bone and the deltopectoral surface is turned downward as in *Pucadelphys*; finally, a clear sulcus also separates the entepicondyle and trochlea, without however articulating with the upper lip of the ulna. The situation is the same in *Philander* and *Monodelphis*, whose humerus is very close to that of *Pucadelphys* in every aspect: proportions, triangular and deflected deltopectoral surface, high supinator ridge, and distal width with a third articular surface. That of *Perameles* also shows a deflected deltopectoral surface, but the bone is even stouter, the supinator ridge less high and a supratrochlear foramen is present.

An interesting feature in the humerus of *Pucadelphys* is the great development of the areas for the extensors of the forearm and the carpus, although it is relatively no greater than in terrestrial didelphids such as *Monodelphis* or *Metachirus*. To be noted is the difference between the humeri of these last two forms, both terrestrial, but with some saltatorial capabilities in *Metachirus*.

Ulna - Radius. — The ulna and radius of *Henkelotherium* are slightly longer than the humerus; the proportions are not clear in *Pucadelphys* since the distal epiphyses of these two bones are not preserved, but they appear to have been subequal; the two elements are about equal in *Didelphis* and *Metachirus*. In *Henkelotherium*, the ulna and radius were more slender and closely appressed over the whole length; another notable difference is the stronger olecranon and the deeper sigmoid incisure than in *Pucadelphys*. In *Barunlestes* the two bones have proximally an anteroposterior position relative to each other, a position more typical of metatherians than of eutherians. The olecranon is "slightly bent forwards" (KIELAN-JAWOROWSKA, 1978) like in *Pucadelphys*, but it is shorter, notched anteriorly and terminated by a tubercle; the beak of the olecranon is extended internally in a lip which is absent in *Pucadelphys*.

In *Metachirus* the ulna is more gracile and the olecranon shorter than in *Pucadelphys*, and there is an even more developed upper internal lip above the greater sigmoid cavity, as in *Barunlestes*; also the lesser sigmoid cavity is more distinct and hollow. The same remark concerning the upper lip applies to *Didelphis*; on the contrary, in *Monodelphis* the internal lip is

Source : MNHN, Paris

reduced: it thus seems that, contrary to OSGOOD's statement, there is no relationship between the presence of an internal articular surface on the distal extremity of the humerus (present in *Monodelphis*) and the presence of an internal upper lip on the ulna; the latter may also correspond to an extension of the surface for the digit flexor muscles. In *Monodelphis*, the bone is again more gracile than in *Pucadelphys*, but the olecranon is as high and the morphology very similar. The olecranon is particularly high in *Philander*, but the bone is rather stout.

In *Barunlestes*, the proximal surface of the radius is much more complex than in *Pucadelphys*, this time in a eutherian fashion. In *Metachirus*, *Monodelphis* and *Didelphis*, this surface is similar to that of *Pucadelphys* but more rounded. In the latter, the diameter of the radius relative to that of the ulna comes closer to that of *Metachirus* and *Monodelphis* than to *Didelphis*, but the bones are relatively more stout.

In *Metachirus* and *Didelphis*, the ulna and radius remain slightly apart for the whole length in the latter and for the upper third in the former, *Metachirus* being thus closer in this respect to *Pucadelphys*. The two bones remain somewhat more apart in *Monodelphis*, the radius being more curved. *Perameles* is very specialized in this area and not comparable to the other forms examined here.

In conclusion, the general stoutness of the ulna and radius in *Pucadelphys* can be considered as primitive, and no particular morphological specialization distinguishes these bones from those of living terrestrial didelphids.

PELVIC GIRDLE (Figs 31A, 41, 42 and 47B; Table 13).

Three elements: 6106, complete, ventral view; 6110, left ilium (all views) and ischium (external view) - part of right ilium and ischium (internal view); 6111, nearly complete, left and right ilium and ischium, dorsal view.

The suture between the ilium and ischium is clear dorsally, that between the ischium and pubis clear ventrally, but that between ilium and pubis is less distinct.

Ilium. —The ilium forms a little more than half the length of the pelvis, which makes it relatively short; its main characteristics are the strong anterior eversion, the thinness and the dorsoventral expansion of the anterior part. It is an elongated, spatula-shaped bone, with a deep dorsoventral iliac wing, and a long but not so deep iliac body. The iliac wing flares anterolaterally; the dorsal border is acute, the ventral border even more so and the iliac crest which unites them anteriorly is rounded and thin. The lateral (gluteal) surface is concave laterally in the longitudinal direction; more laterally and dorsoventrally, the wing is divided by an oblique crest into a concave lateroventral (iliac) surface (Fig. 42, i s) and a convex lateral surface. The internal surface is uniformly concave for vertebral muscles (anterior half) and for the sacral rib more distally (auricular half); the entire iliac wing remains thin.

The much thicker iliac body is narrower dorsoventrally, but flares somewhat distally in front of the acetabulum (a c); its ventral (iliac) face (i f) is well delimited and rounded. The dorsolateral face is slightly concave, and the endopelvic face deeply concave. The dorsal border joins the iliac wing by a deep notch, the great sciatic (g s n). Details of the acetabulum are not observable, the cavity being filled in all cases with the femoral head; the majority of the cavity is ischiatic.

Ischium.— The ischium is nearly as long as the ilium, extending posteriorly from the ilium

Source : MNHN, Paris

as a thick longitudinal branch which flattens distally. In dorsal view this branch is twisted, the medial border becoming dorsolateral (long sciatic spine (s s) plus weakly concave sciatic notch) and at the same time the medial face becomes dorsal. The ventral face of the same branch is slightly convex immediately behind the acetabulum and the cotyloid notch; it becomes flat posteriorly on

FIG. 41. — *Pucadelphys andinus*. Stereophotos. 6106, pelvis and L3-C6, ventral view; right tibia, fibula and tarsus, external view. X 3.

FIG. 41. — Pucadelphys andinus. *Stéréophotos. 6106, pelvis et L3-C6, vue ventrale; tibia, péroné et tarse droits, vue externe. X 3.*

Source : MNHN, Paris

both sides; the distal branch is wide and flat and makes a right angle with the longitudinal branch. The ischiatic participation to the symphysis is not known since the suture between pubis and ischium is not visible at that level. The ischiatic tuberosity (i t) is little pronounced. There is no obturator tubercle.

Pubis. — The two branches of the pubis make an obtuse angle one with the other; the acetabular branch is relatively narrow and the longitudinal branch even narrower. There is only a weak pectineus tubercle (p t) at the ilio-pubic junction. The obturator foramen (o f) is obliquely elongated and the pubic symphysis (s) relatively long. There is no pubic tubercle at the anterior junction of the two pubes.

Os marsupium.—The os marsupium (nearly complete left and right in 6106; proximal part of right in 6111) is a long, thin, flat and relatively short bone that is broad basally, where it occupies only about 40% of the anterior pubic border; it tapers proximally and bends slightly laterally (Fig. 41; Table 14).

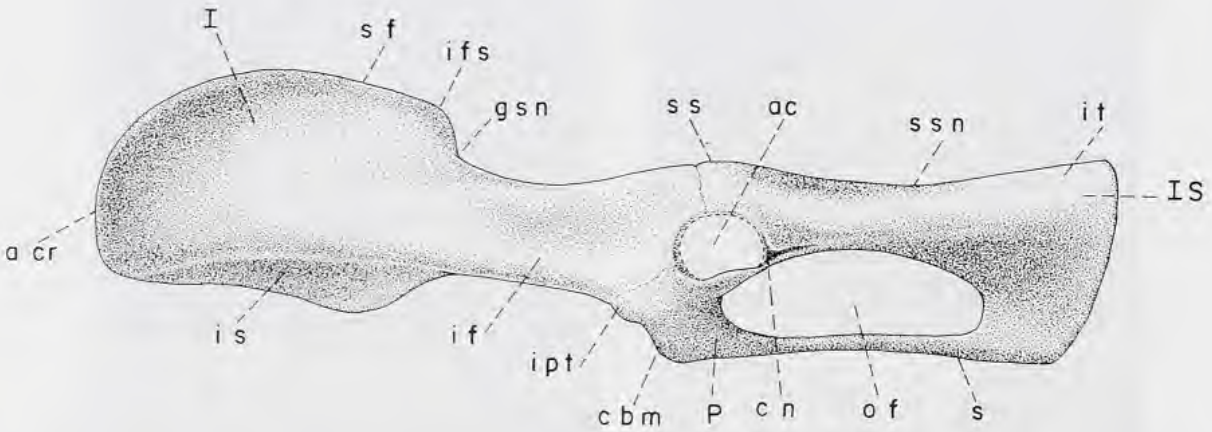


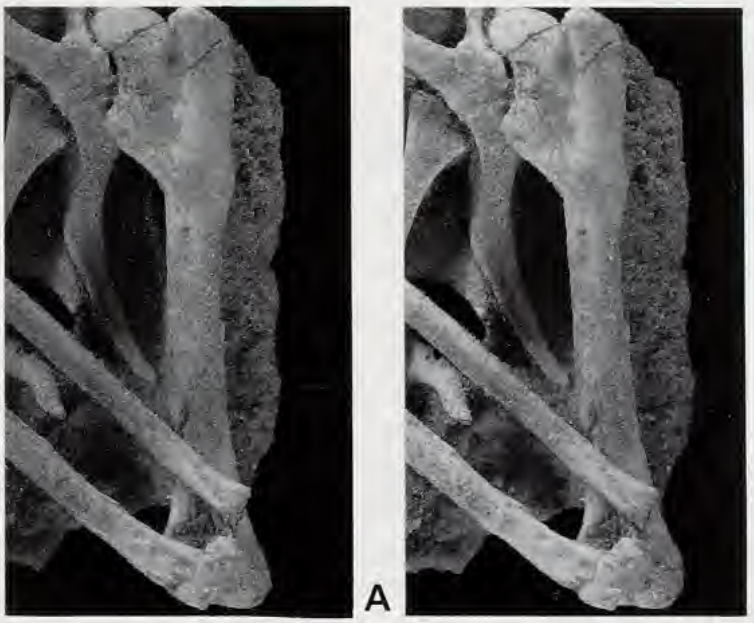
FIG. 42. — *Pucadelphys andinus*. 6106 and 6111 combined, left lateral face of pelvis, restored. X 5. Abbreviations: **I**, ilium; **IS**, ischium; **P**, pubes. **ac**, acetabulum; **a cr**, anterior crest; **c b m**, contact border for os marsupium; **c n**, cotyloid notch; **g s n**, great sciatic notch; **i f**, iliac face; **i f s**, inferior posterior spine; **i s**, iliac surface; **i t**, ischiatic tuberosity; **o f**, obturator foramen; **s**, symphysis; **s f**, sacral face; **s s**, sciatic spine; **s s n**, small sciatic notch.

FIG. 42. — Pucadelphys andinus. *Face latérale gauche du bassin (reconstruction basée sur 6106 et 6111). X 5. Abréviations:* ***I****, ilion;* ***IS****, ichion;* ***P****, pubis;* ***ac****, acetabulum;* ***a cr****, crête antérieure;* ***c b m****, bord de contact pour l'os marsupial;* ***c n****, incisure cotyloïde;* ***g s n****, grande incisure sciatique;* ***i f****, face iliaque;* ***i f s****, épine inférieure postérieure;* ***i s****, surface iliaque;* ***i t****, tubérosité ischiatique;* ***o f****, foramen obturateur;* ***s****, symphyse;* ***s f****, face sacrée;* ***s s****, épine sciatique;* ***s s n****, petite incisure sciatique.*

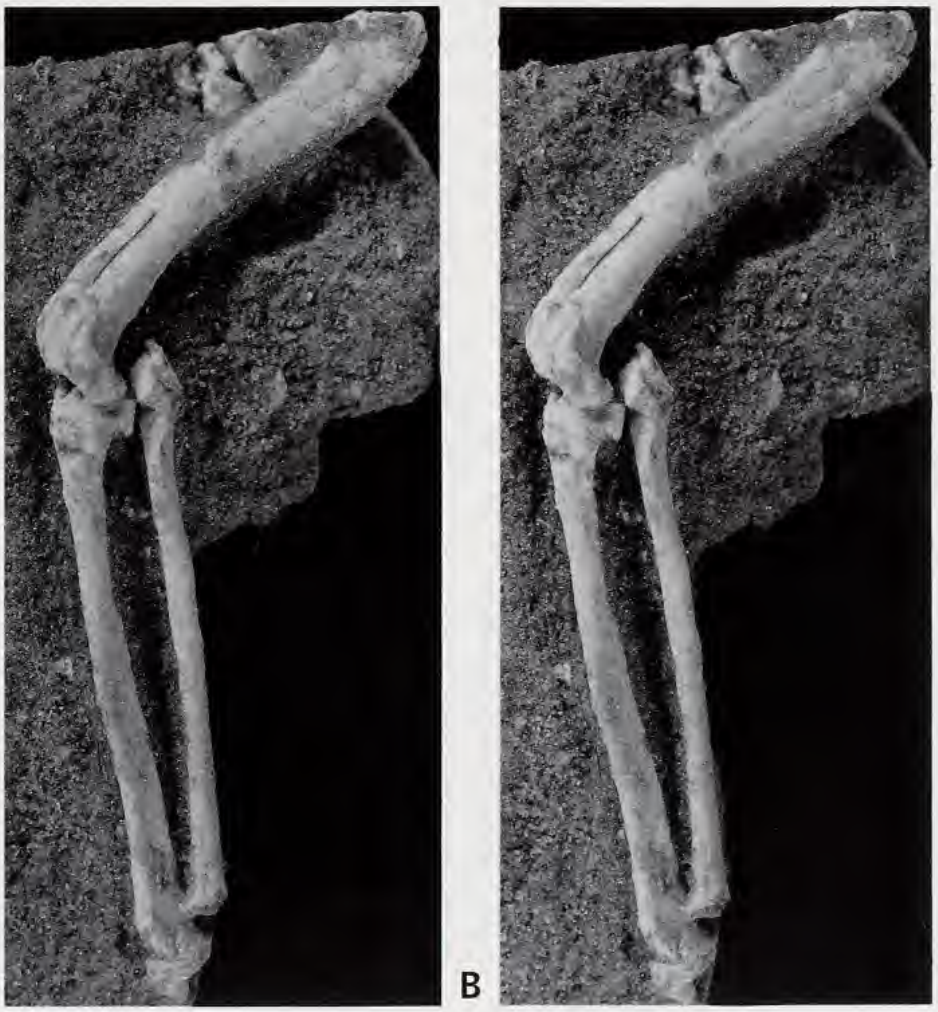
FIG. 43. — *Pucadelphys andinus*. Stereophotos. A, 6106, right femur, posterior view; partial tibia and fibula, external view, X 3; B, 6105, left femur, tibia and fibula, external view. X 3.

FIG. 43. — Pucadelphys andinus. *Stéréophotos. A, 6106, fémur droit, vue postérieure; tibia et péronés, vue externe. X 3; B, 6105, fémur gauche, tibia et péroné, vue externe. X 3.*

Source : MNHN, Paris



A



B

Source : MNHN, Paris

Hindlimb

Femur (Figs 43, 44, 45C and 47A; Table 15). — Seven elements: 6105, left, missing proximal end, anterior and external views; 6106, complete left, posteroexternal view - complete right, posterior view; 6110, complete right, posterior and both lateral views - complete left, anterior and partly posterior views; 6111, complete left, anterior, posterior and external views - complete right, anterior and external views.

The femur is slightly longer than the humerus; it is practically straight, and greatly expanded proximally.

The head (Fig. 44, h) is wide, hemispherical, and its base is circumscribed by a suture line. A very shallow fovea capitis for the ligamentum teres is visible, in an excentric position. The neck is very short, making an angle of 40° with the diaphysis. The greater trochanter (g t) is slightly bent anterointernally; it does not reach the level of the top of the head but only that of its sutural base; it is broad and borders externally the deep trochanteric fossa (t f); a marked and short ridge delimits the latter externally; but no clear intertrochanteric ridge delimits it internally, only a marked bump (tc c). The lesser trochanter (l t) is particularly large, lamellar and V-shaped with the apex directed internally; a notch joins it with the base of the head. The third trochanter (t t) is represented by a modest swelling on the external face of the diaphysis situated across from the distal edge of the lesser trochanter.

On the anterior face, the bone is extremely concave under the crest of the greater trochanter, then convex except for a sulcus along the edge of the external border. Further down, the diaphysis is ovoid in cross-section, with an anterior flattening.

On the distal end, the condyles protrude posteriorly as usual; the external condyle (e c) is wider transversely and the internal condyle (i c) longer anteroposteriorly; but they reach about the same level distally. Anteriorly, the patellar fossa is high, wide and shallow. The external trochlear crest is slightly sharper than the internal one. The susepicondylar tubercles (s c t) are modest but distinct.

Patella. — There is no evidence of an ossified patella.

Tibia (Figs 41, 43, 45, 46, 47A and 48; Table 16). — Six elements: 6105, complete left, external view; 6106, complete right, external view - complete left (except for small part of diaphysis), internal view; 6110, proximal half of left, external view; 6111, left, external view - right, posterior view.

The tibia is slightly longer than the femur. The diaphysis is nearly straight (at least as preserved), although in anterior view the tibial crest has a slight sigmoidal curve. On the proximal surface, the interarticular spine is higher than the two lateral articular facets, of which the external one (Fig. 46, e f) is the larger. The anterior, external and internal tuberosities are not very prominent; a distinct fibular facet (f f) occurs on the posteroexternal surface, just below the external articular facet which overlaps the shaft. Proximally, the diaphysis is triangular in cross section (apex anterior), while distally it is flattened externointernally, but it remains relatively wide anteroposteriorly. The external surface is flat proximally, then transversely concave distally; the internal surface, barely convex proximally, becomes flat distally. Posteriorly and proximally,

Source : MNHN, Paris

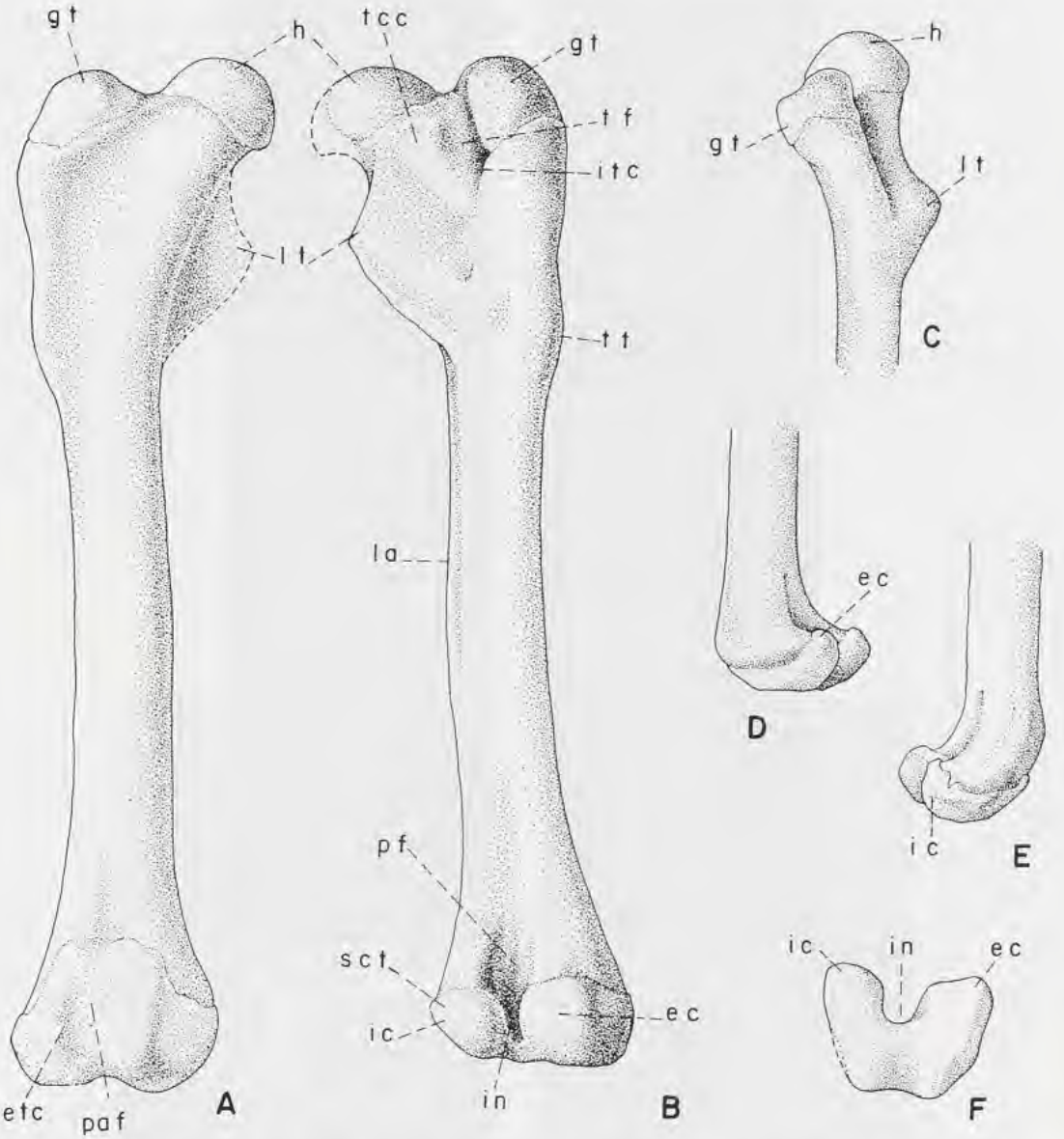
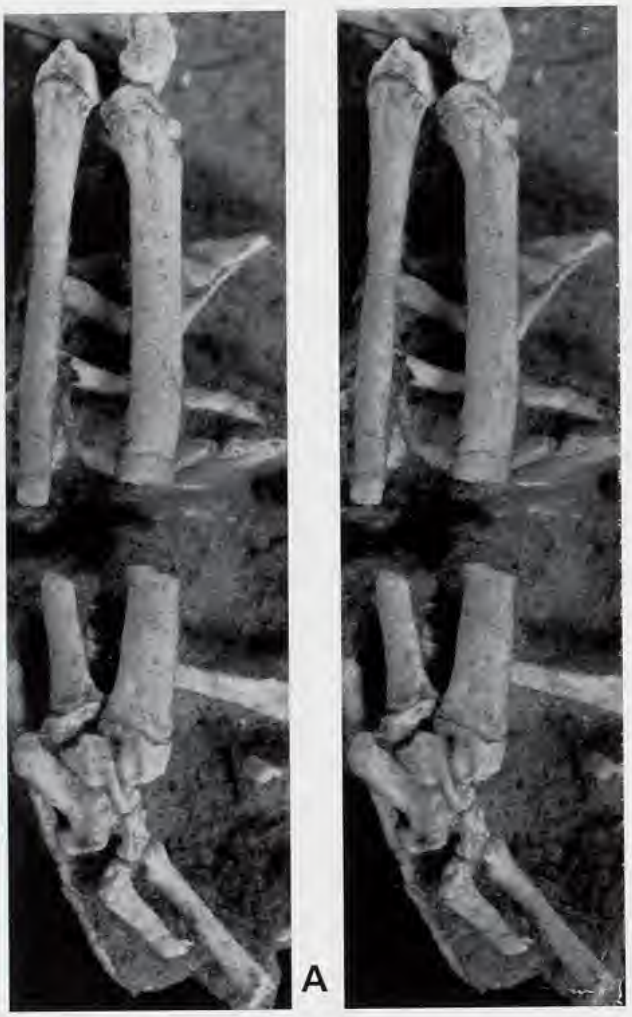


FIG. 44. — *Pucadelphys andinus*. Femur, partly restored: A, anterior face of right (combined left and right 6106 and 6110); B, posterior face of right (combined left and right 6106 and 6110); C, external face of right proximal end (6110+6111); D, external face of left distal end (left 6111 and right 6110 reversed); E, 6110, distal surface of right; F, 6106, internal view of left distal end. X 5. Abbreviations: **e c**, external condyle; **e t c**, external trochanteric crest; **g t**, greater trochanter; **h**, head; **i c**, internal condyle; **i n**, intercondylar notch; **i t c**, intertrochanteric crest; **l a**, ligne âpre; **l t**, lesser trochanter; **p f**, popliteal fossa; **pa f**, patellar fossa; **s c t**, sus-condylar tubercle; **t c c**, bump (voir texte); **t f**, trochanteric fossa; **t t**, third trochanter.

FIG. 44. — Pucadelphys andinus. *Fémur partiellement restauré: A, face antérieure du fémur droit (reconstitution basée sur 6106 et 6110); B, face postérieure du fémur droit (basée sur 6106 et 6110); C, face externe de l'extrémité proximale droite (basée sur 6110 et 6111); D, face externe de l'extrémité distale gauche (basée sur le spécimen 6111 gauche et le spécimen 6110 droit renversé); E, 6110, surface distale du fémur droit; F, 6106, vue interne de l'extrémité distale gauche. X 5. Abréviations: **e c**, condyle externe; **e t c**, crête trochantérienne externe; **g t**, grand trochanter; **h**, tête; **i c**, condyle interne; **i n**, échancrure intercondylienne; **i t c**, crête intertrochantérienne; **l a**, ligne âpre; **l t**, petit trochanter; **p f**, fosse poplitée; **pa f**, fosse patellaire; **s c t**, tubercule sus-condylien; **t c c**, bosse (voir texte); **t f**, fosse trochantérienne; **t t**, troisième trochanter.*

Source : MNHN, Paris



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there is a wide and deep vertical depression; a faint "ligne oblique", which separates the popliteal surface from that for the flexor digitorum, continues to the mid-length of the bone. Distally, the bone widens somewhat; the internal malleolus (i m) projects slightly more distally than the external malleolus (e m) of the fibula. The distal articular surface itself is not accessible.

Fibula (Figs 41, 43, 45, 46A, 47A and 48; Table 17). — Six elements: 6105, complete left (except for distal epiphysis), posterior and external views; 6106, complete right, posteroexternal view - left, anteroexternal view; 6110, proximal half of left, external view; 6111, greater part of left, anterointernal view - nearly complete right (lacking only distal epiphysis), internal view.

The fibula is slightly shorter and more slender than the tibia. The two bones are completely separated. The fibula flattens somewhat proximally and distally, while remaining relatively robust at mid-length; at that level, it is semi-circular in cross-section. Proximally the styloid apophysis (Fig. 46, s a) is prominent; a distinct tibial facet occurs on the internal face making a salient lip, and the bone is strongly concave posteroexternally for a short distance. At the distal end, there is a broad internal facet for the astragalus (a f) and the external malleolus (e m) is well developed.

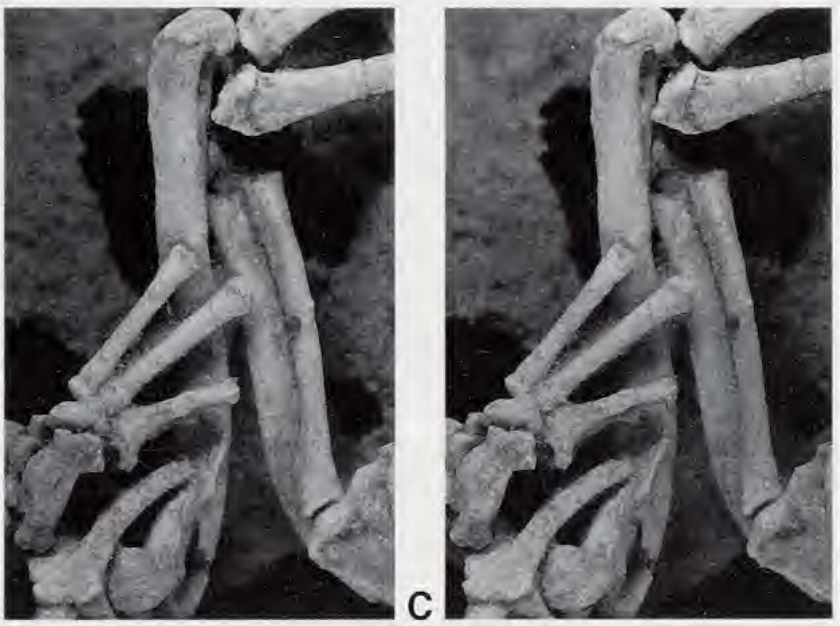

FIG. 45. — *Pucadelphys andinus*. Stereophotos. A, 6106, left tibia and fibula, tarsals and two metatarsals, internal view. X 3; B, 6105, left tibia and fibula, lateral view. X 3; C, 6106, left femur, proximal part of tibia and fibula (top), internal view; ulna and radius (bottom), anterior view, and right foot, dorsal view. X 3.

FIG. 45. — Pucadelphys andinus. *Stéréophotos. A, 6106, tibia et péroné gauches, tarsiens et deux métatarsiens, vue interne. X 3; B, 6105, tibia et péroné gauches, vue latérale. X 3; C, 6106, fémur gauche, partie proximale du tibia et du péroné (en haut), en vue interne; cubitus et radius (en bas), en vue antérieure, et pied droit, en vue dorsale. X 3.*

Source : MNHN, Paris

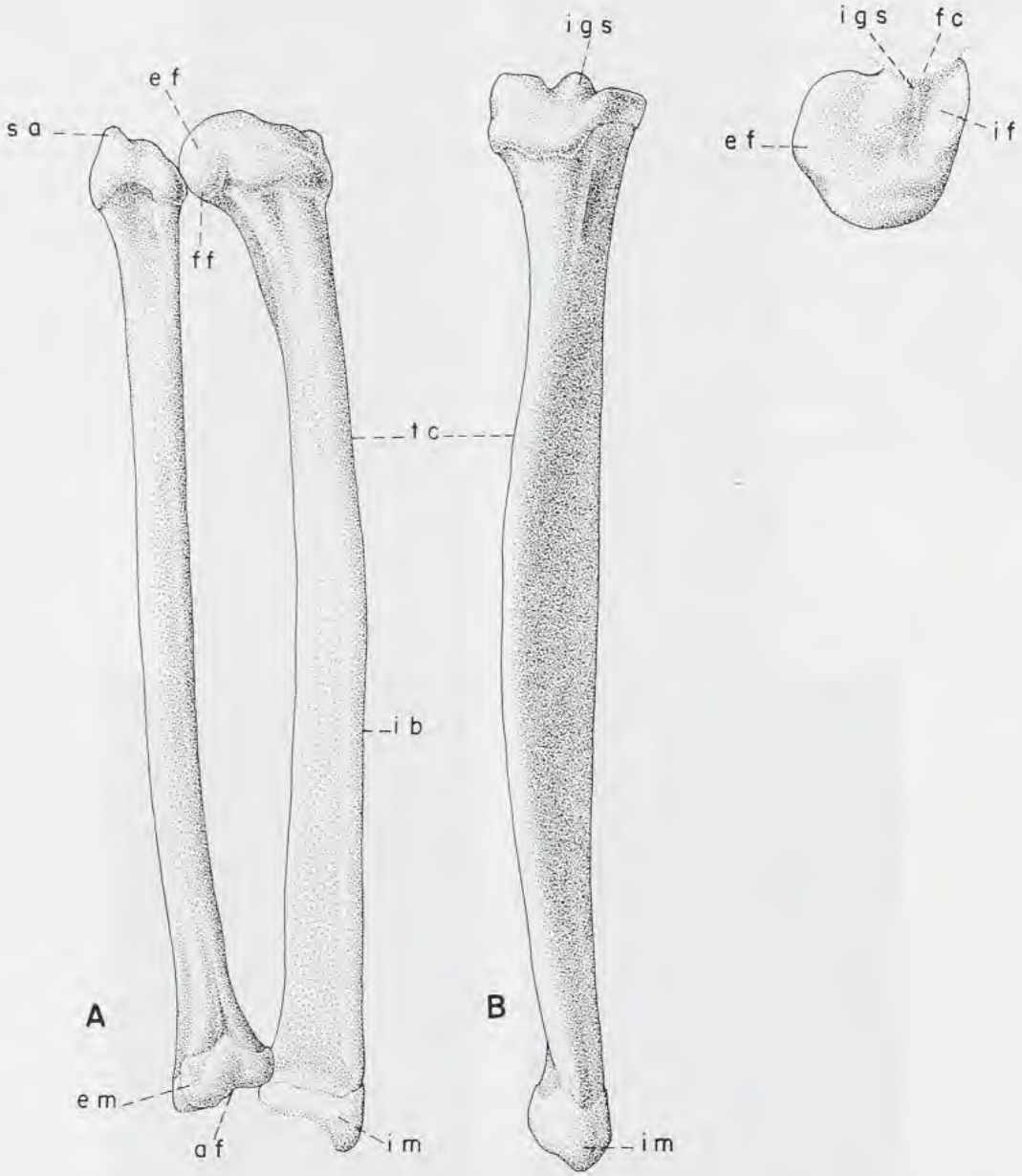

FIG. 46. — *Pucadelphys andinus*. A, 6106, right tibia and fibula, anteroexternal face; B, 6106, right tibia, anterior face; C, 6106, right proximal surface. X 5. All drawn as preserved. Abbreviations: **a f**, astragalar facet; **e f**, external facet; **e m**, external malleolus; **f c**, femoral condyle; **f f**, fibular facet; **i b**, interosseous border; **i f**, internal facet; **i g s**, interglenoid spine; **i m**, internal malleolus; **s a**, styloid apophysis; **t c**, tibial crest.

FIG. 46. — Pucadelphys andinus. *A, 6106, tibia et fibula droits, face antéro-externe; B, 6106, tibia droit, face antérieure; C, 6106, tibia droit, surface proximale. X 5. Dessins en l'état de conservation. Abréviations:* ***a f****, facette astragalienne;* ***e f****, facette externe;* ***e m****, malléole externe;* ***f c****, condyle fémoral;* ***f f****, facette fibulaire;* ***i b****, bord interosseux;* ***i f****, facette interne;* ***i g s****, épine interglénoïde;* ***i m****, malléole interne;* ***s a****, apophyse styloïde;* ***t c****, crête tibiale.*

Source : MNHN, Paris

Pes

Elements of the pes that include some tarsals and associated metatarsals are represented on the left and right sides of 6106. Reference of these elements to the pes is certain because the tarsals remain articulated with the tibia and fibula. Two other element groupings (6105 left, 6110 left) are also cautiously assigned to the pes because of their possible relationships with tibia and fibula, although in these cases they are not directly articulated with these bones. The elements common to these two last groupings are indistinguishable, but the ?cuboids of 6110 are not identical to those of 6106 and the ?metatarsals of 6105 are generally shorter and more robust than in 6106. We attribute these differences to individual variation, but because the cuboid of the pes and unciform of the manus are very similar in didelphids, we are unable to state decisively that the elements in 6105 and 6110 are not, in fact, of the manus.

Astragalus (Figs 41, 45A and C, and 48). — Three elements: 6106, left, dorsal view—right, partial ventral view; 6111, left, ventroposterior view. All three specimens are displaced and squeezed between the distal ends of the tibia and fibula on one hand, and the calcaneum on the other, and thus are distorted and give only partial views of the bone.

It appears that no neck separated the "head" from the "body": the former is only partly visible. Dorsally, a continuous ridge (the medial trochlear crest) separates the inner malleolar facet (Fig. 48, i m f), deep and elongated, from the tibial or trochlear facet (t f); the latter is shallow. A ridge essentially parallel to the first but weaker and shorter (the lateral trochlear crest) isolates a concave fibular facet (f f) on the external side of the astragalus. For the plantar face, and if one interprets correctly 6111, the concave surface corresponding to the calcaneum (CaA of SZALAY, 1982) is high and narrow, and limited distally by a condyle; a wide interosseus sulcus separates the CaA from the distal condyle, where the surfaces for the sustentaculum tali, and for the navicular more distally, are practically continuous one with the other.

Calcaneum (Figs 41, 45A and C, 48, 49, 50 and 51; Table 18). — Five elements: 6105, complete left, isolated, all views; 6106, nearly complete right, external view - nearly complete left, ventral view; 6110, nearly complete right, isolated, all views; 6111, incomplete left, external view.

The following description is based on 6105 left (Fig. 49). The posterior half or heel accounts for almost 50% of the total length of the calcaneum; it curves internally at the posterior end. It is high dorsoventrally and narrow from side-to-side; the dorsal border is even narrower than the ventral one. It terminates with a robust tuber calcanei (t c), the posterior face of which slopes anteroventrally; the medial side is more bulbous than the lateral. The anterior half of the calcaneum is subequal in length and breadth. The dorsal surface is dominated by a high, ovale tuberosity for one of the two calcaneo-astragalar facets (CaA); medial to it is a broad shelf, the sustentaculum tali (s t), supporting the small and ill-defined second calcaneo-astragalar facet; close to the CaA is the narrow, anteroposteriorly elongate sulcus calcanei (s c), pierced by a tiny vascular foramen. The long axis of the CaA is oblique relative to the axis of the heel (~45°); its surface itself is convex, more so on the external side, and no clear fibular surface (CaFi) is discernible (unless the external border of this facet is for the fibula?). Anterior to the CaA is a notable expansion, the distal process

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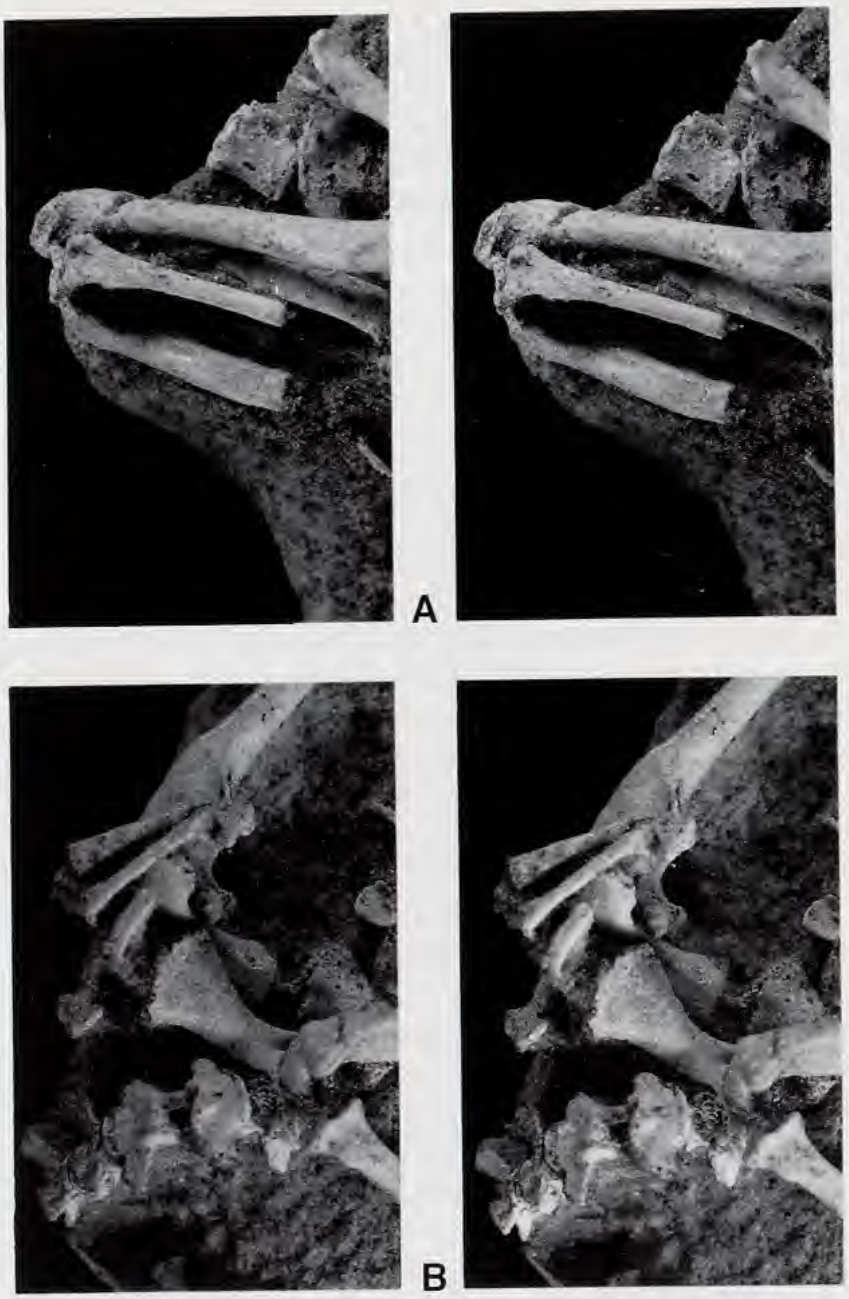

FIG. 47. — *Pucadelphys andinus*. Stereophotos. A, 6110, right femur, external view; half tibia and fibula and last thoracic vertebra, ventral view. X 3; B, 6110, proximal part of left femur, left ischium, right cuboid and metatarsals II, III, IV, dorsal view. X 3.

FIG. 47. — Pucadelphys andinus. *Stéréophotos. A, 6110, fémur droit, vue externe; demi-tibia et péroné et dernières vertèbres thoraciques, vue ventrale. X 3; B, 6110, partie proximale du fémur gauche, de l'ischion gauche, du cuboïde droit et des métatarsiens II, III, IV, vue dorsale. X 3.*

Source : MNHN, Paris

(d p), which is slightly convex dorsally, a convexity limited internally by a strong concavity, but the sulcus for the tendon of the peroneus brevis is poorly defined (gt pb). The concavity is limited externally by a rounded rim corresponding to a well developed peroneus process (p p) (somewhat incomplete on the specimen). The edge of the distal and peroneal processes limit dorsally the cuboidal facet (c f).

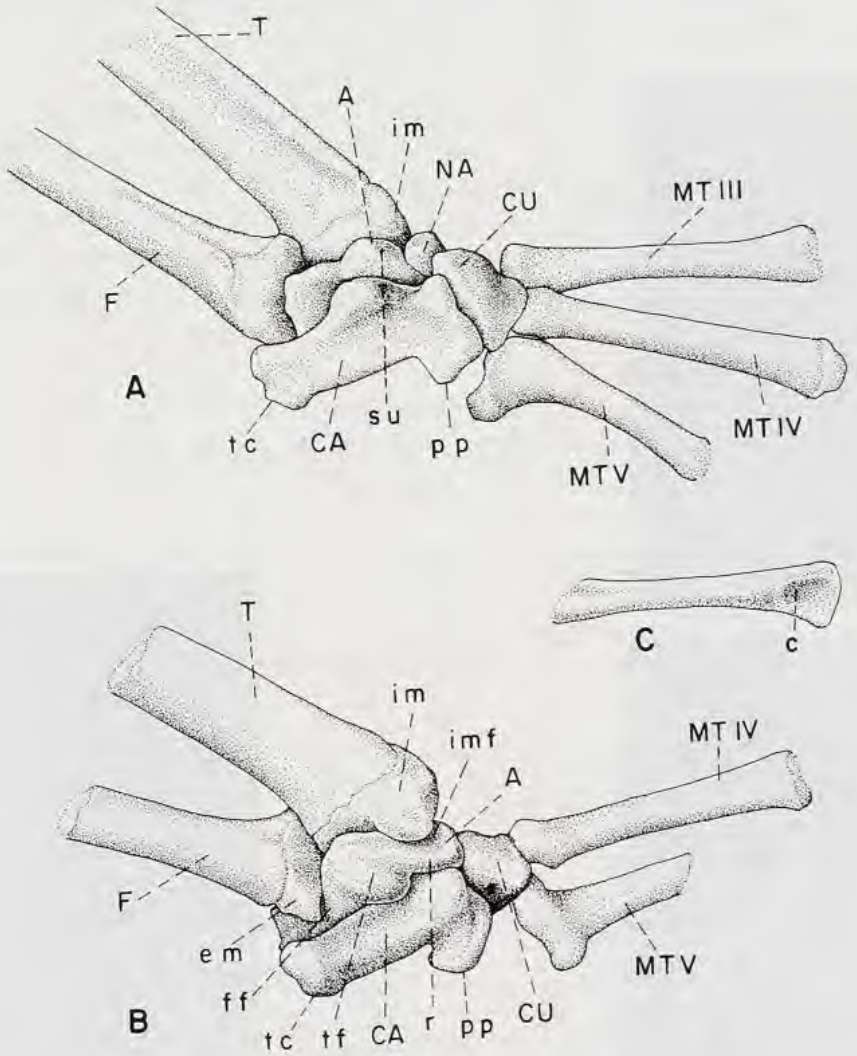

FIG. 48. — *Pucadelphys andinus*. A, 6106, right pes, dorsal face; B, 6106, left pes, ventrolateral face; C, 6110, left metatarsal III, proximal extremity, external face. X 5. Drawn as preserved. Abbreviations: **A**, astragalus; **CA**, calcaneum; **CU**, cuboid; **F**, fibula; **MT**, metatarsal; **NA**, navicular; **T**, tibia; **c**, cavity for adjacent metatarsal; **e m**, external malleolus; **f f**, fibular facet; **i m**, internal malleolus; **i m f**, inner malleolar facet; **p p**, peroneal process; **r**, ridge, see text; **su**, sustentacular condyle; **t f**, trochlear facet.

FIG. 48. — Pucadelphys andinus. *A, 6106, pied droit, face dorsale; B, 6106, pied gauche, face ventro-latérale; C, 6110, métatarsien III gauche, extrémité proximale, face externe. X 5. Dessins en l'état de conservation. Abréviations:* **A**, *astragale;* **CA**, *calcanéum;* **CU**, *cuboïde;* **F**, *péroné;* **MT**, *métatarsien;* **NA**, *naviculaire;* **T**, *tibia;* **c**, *cavité destinée au métatarsien adjacent;* **e m**, *malléole externe;* **f f**, *facette fibulaire;* **i m**, *malléole interne;* **i m f**, *facette malléolaire interne;* **p p**, *processus péronéen;* **r**, *côte, voir texte;* **su**, *condyle sustentaculaire;* **t f**, *facette trochléaire.*

Source : MNHN, Paris

In plantar (ventral) view, the peroneal process forms a triangular point anteriorly; it is quite protruding and is bordered internally by a bump (b), the distal plantar tubercle; between the two is a groove, presumably for the digit V abductor. The cuboidal facet is vaguely diamond-shaped and quite shallow; it is inclined from anterior to posterior and external to internal, and nearly perpendicular to the long axis of the bone.

The calcaneum 6110 is smaller than 6105, as is the entire specimen; it is also somewhat abraded. Its main difference concerns the cuboidal facet, which is oriented more internally than distally.

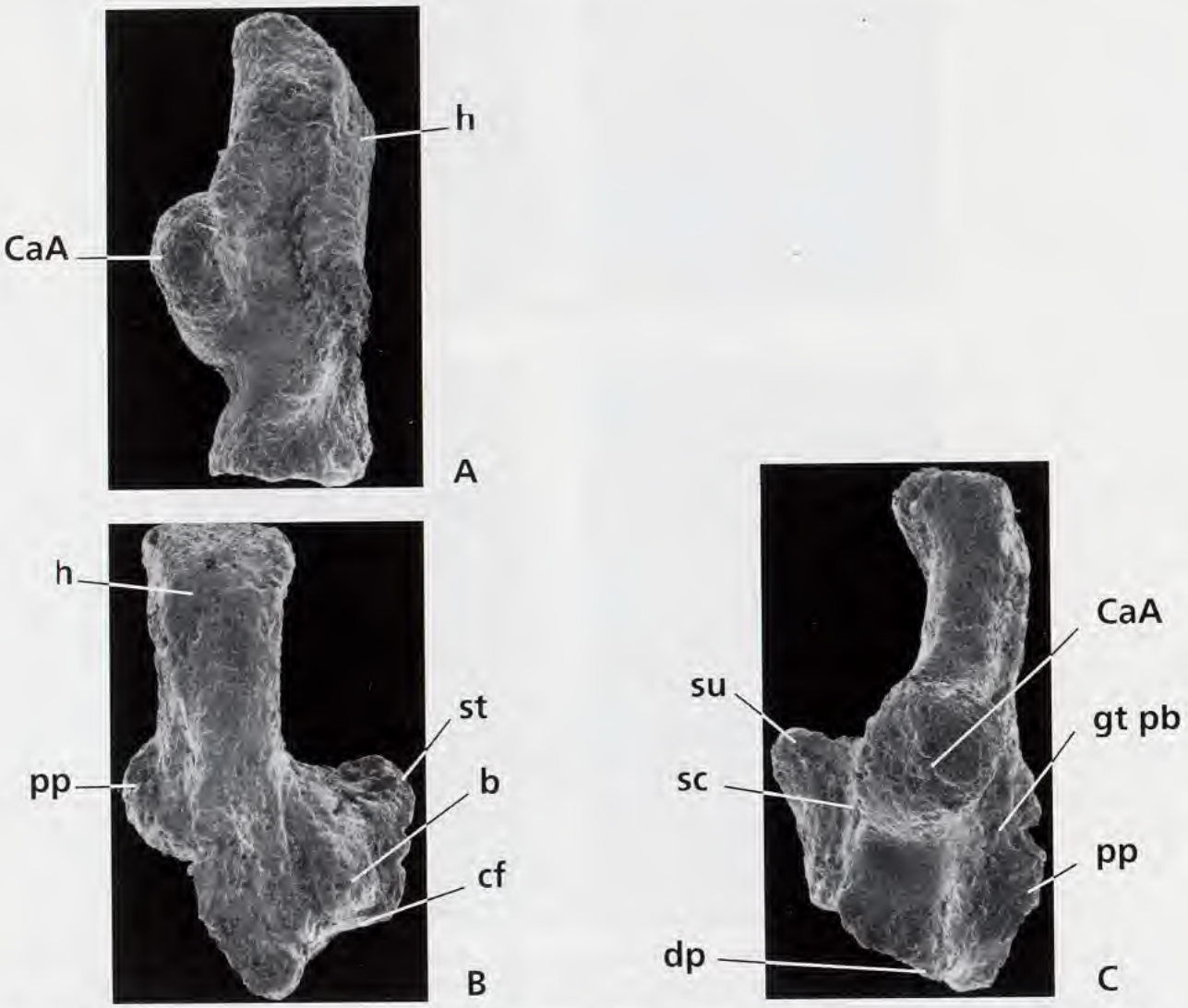

FIG. 49.— *Pucadelphys andinus*. 6105, left calcaneum: A, external face; B, ventral face; C, dorsal face. X 15. Abbreviations: **b**, bump (see text); **CaA**, astragalar condyle; **c f**, cuboidal facet; **d p**, distolateral process; **gt pb**, groove for tendon of peroneus brevis; **h**, heel; **p p**, peroneal process; **s c**, sulcus calcanei; **s t**, sustentaculum tali; **t c**, tuber calcanei.

FIG. 49.— Pucadelphys andinus. *6105, calcanéum gauche: A, face externe; B, face ventrale; C, face dorsale. X 15. Abréviations: **b**; bosse (voir texte); **CaA**, condyle astragalien; **c f**, facette cuboïdienne; **d p**, processus disto-latéral; **gt pb**, sillon pour le tendon du peroneus brevis; **h**, talon; **p p**, processus péronéen; **s c**, sulcus calcanei; **s t**, sustentaculum tali; **t c**, tuber calcanei.*

Source : MNHN, Paris

Navicular (Figs 4, 41, 45C and 48). — One element: 6106, right, complete but partly hidden by adjacent bones.

Cuboid (Figs 45A and C, 48 and 52; Table 19). — Two certain elements: 6106, right, dorsal view—left, plantar view. Two uncertain elements: 6110 right, all views except ventral; and 6105 left, dorsal and external views.

The cuboids of 6106 show a triangular dorsal face (Fig. 52C), with a distal base articulating with the whole surface of metatarsal IV and a small part of metatarsal V (su IV-V). This dorsal face is almost flat; its internal border is slightly indented for the cuneiform. Proximally a crest separates the internal and external surfaces: the former is deep, flat and quadrangular. The external face (Fig. 52B), articulated for more than the proximal half with the calcaneum (c s), and dorsally with the navicular (n s) seems to be almost flat; the distal half of this external face bears two tuberculae separated by a deep pit for the tendon of the peroneus longus muscle (t p l). Finally, the ventral face seems to be narrow and convex from side-to-side.

The cuboid? of 6110 differs essentially in its proportions, being stouter, and also in the calcanear facet, which is clearly convex proximodistally. The dorsoexternal bump is much more protruding than the ventral one. These differences may be attributed to better preservation of the bone in 6110. On the distal face, the facet for metatarsals IV and V forms a broad triangle; no relief delimitates the respective facets for these two metatarsals; however, that for metatarsal V must have been very narrow. A very small astragalar facet is discernible on the proximal corner.

Cuneiform IV? (Figs 5 and 52A, C; Table 19). — One element: 6110, left, dorsal and internal views.

It is transversely narrow, short, concave and recurved mesially for contact with cuneiform III, convex laterally for the cuboid. It seems to bear a proximal bump ventrally.

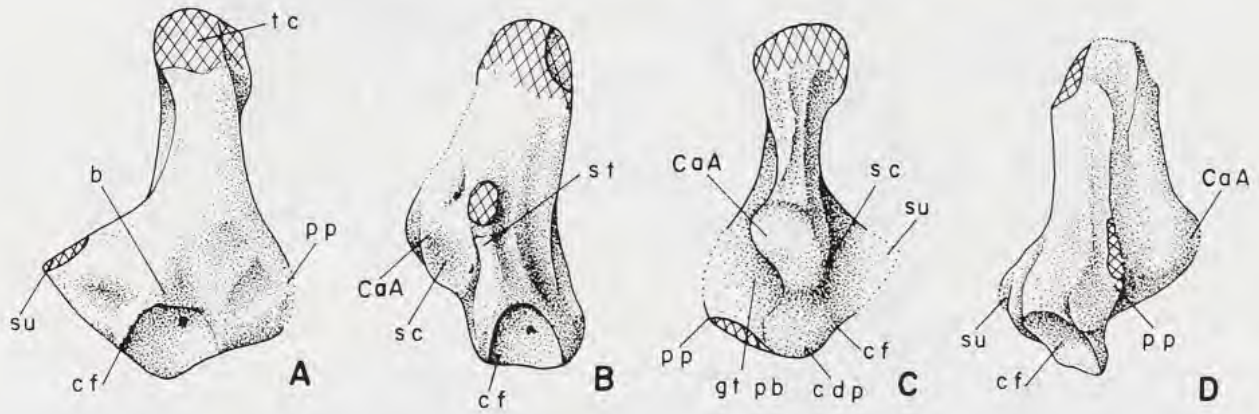

FIG. 50. — *Pucadelphys andinus*. 6110, right calcaneum: A, plantar view; B, internal view; C, dorsal view; D, external view. X 9. Drawn as preserved. Abbreviations: see caption to Fig. 49.

FIG. 50. — Pucadelphys andinus. 6110, calcanéum droit: A, vue plantaire; B, vue interne; C, vue dorsale; D, vue externe. X 9. Dessins en l'état de conservation. Abréviations: voir légende Fig. 49.

Source : MNHN, Paris

Metatarsals (Figs 4B, 33B, 45A and C, 47B and 48; Table 20). — Represented in four specimens: 6105?, left, II-V, dorsal view; 6106, right, III-V, dorsal view - left, IV and proximal half of V, dorsal view; 6110?, left, II, III and distal part of IV, dorsal view.

As mentioned above, the relative robustness of the left metapodials of 6105 compared to the undisputable metatarsals of 6106 (though of lesser amplitude than the discrepancy observed between the foot and hand of *Didelphis*) led us to suspect the reference of these metapodials to the manus rather than pes. Nevertheless, we cautiously choose to interpret this difference as individual variation.

In length, the middle metatarsals (II, III, IV) are about one third the length of the tibia-fibula; metatarsals III and IV are subequal in length, II is slightly shorter and V is the shortest. On II to IV, the distal end is broader than the proximal; V differs in having, proximally, a broad laterally directed flange (extending well beyond the cuboidal articulation) while its distal end is narrower. The shape of these distal ends is similar for III and IV; but on II the mesial side is expanded and on V the lateral side is expanded; this end is strongly convex with a deflection on each side, and a depression dorsally and ventrally. On II to IV the diaphysis is subrounded in cross-section at mid-

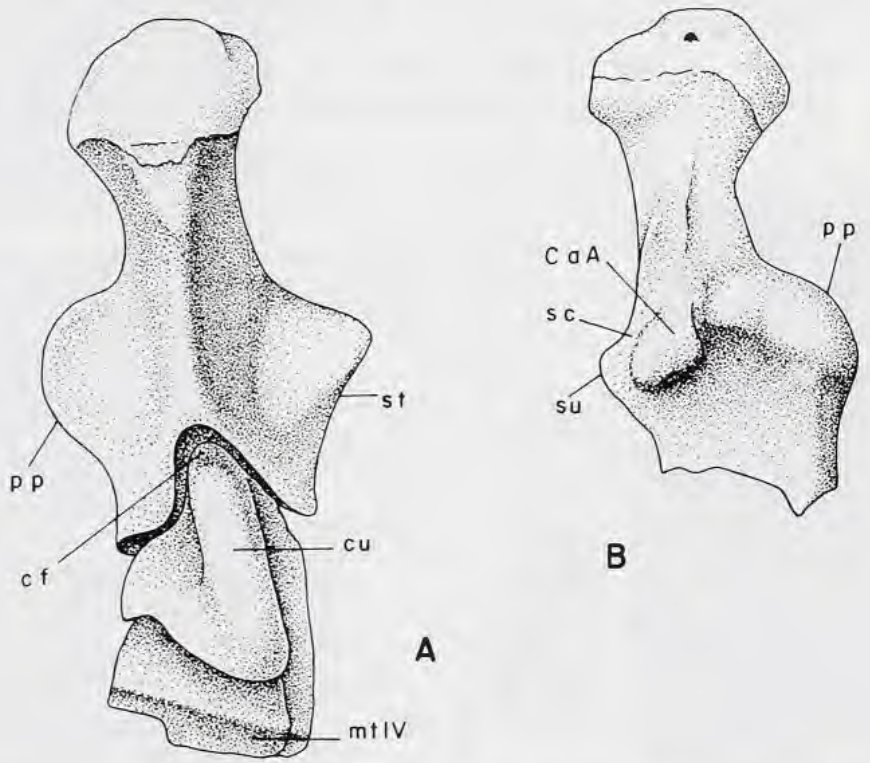

FIG. 51. — *Didelphis*. Left calcaneum: A, plantar view (with cuboid); B, dorsal view. X 3. Abbreviations: **CaA**, astragalar condyle; **cu**, cuboid process; **mtIV**, surface for metatarsal IV; **p p**, peroneal process; **s c**, sulcus calcanei; **st**, sustentaculum tali.

*FIG. 51. — Didelphis. Calcanéum gauche: A, vue plantaire (avec cuboïde); B, vue dorsale. X 3. Abréviations: **CaA**, condyle astragalien; **cu**, processus cuboïdien; **mtIV**, surface pour le métatarsien IV; **p p**, processus péronéen; **s c**, sulcus calcanei; **st**, sustentaculum tali.*

Source : MNHN, Paris

length. Internally and proximally each metatarsal is encased in a pit of the previous one (Fig. 48C, c), thus making the pes a rather rigid unit. This arrangement and preservation of the digits II to V suggest that digit I was, at least, partly divergent, hence possibly opposable.

Phalanges (Fig. 33B). — One proximal phalange in 6105 (left). It is about half the length of the metatarsals. The proximal extremity is wider than the distal, which is convex with no lateral deflection; only a pit borders this convexity on each side.

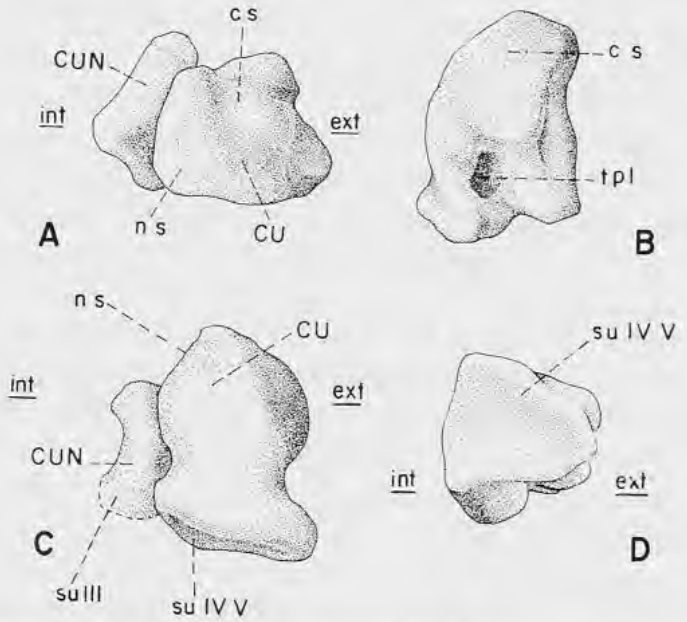

FIG. 52. — *Pucadelphys andinus*. 6110, left ?cuboid and ?cuneiform IV: A, proximal face of both; B, external face of ?cuboid; C, dorsal face of both; D, distal face of ?cuboid. X 9. All drawn as preserved. Abbreviations: **c s**, calcanear surface; **CU**, cuboid; **CUN**, cuneiform; **ext**, external; **int**, internal; **n s**, navicular surface; **suIII**, surface for metatarsal III; **suIV**, surface for metatarsals IV-V; **t p l**, pit for tendon of peroneus longus.

*FIG. 52. — Pucadelphys andinus. 6110, ?cuboïde et ?cunéiforme IV gauches: A, face proximale des deux os; B, face externe du ?cuboïde; C, surface dorsale des deux os; D, face distale du ?cuboïde. X 9. Dessins en l'état de conservation. Abréviations: **c s**, surface calcanéenne; **CU**, cuboïde; **CUN**, cunéiforme; **ext**, externe; **int**, interne; **n s**, surface naviculaire; **suIII**, surface pour le métatarsien III; **suIV**, surface pour les métatarsiens IV-V; **t p l**, fosse pour le tendon du peroneus longus.*

DISCUSSION

Pelvis. — In *Henkelotherium*, the pelvis is very similar to that of *Pucadelphys*, with an elongate ilium and symphysis, a clear incisura acetabuli, and a small participation of the pubis to the acetabulum; however, in *Henkelotherium*, the ilium is relatively longer, apparently not as deep and somewhat thicker, and no posterior iliac spine is developed. The ischium is more robust distally, the obturator foramen relatively smaller, and the stout os marsupium occupies the whole anterior border of the pubis; there is no ilio-pectineus tubercle, which we interpret as the primitive state.

Source : MNHN, Paris

In *Barunlestes,* the main differences with *Pucadelphys* concern the iliac wing, which is relatively longer and narrower, and the wider obturator foramen; the ilio-pectineus tubercle is developed as well as a sciatic spine. There may have been an os marsupium in that genus, as suggested by the presence of a concavity on the anterior margin of the pubis (KIELAN-JAWOROWSKA, 1975).

In *Metachirus*, the ilium is not as everted as in *Pucadelphys*; it is also relatively longer, with a thickened anterior border and a not so deep ventral wing. But the ischium and pubis are very similar to those of *Pucadelphys*, with a similar limitation of the os marsupium to the medial half of the anterior border of the pubis, and an open symphysis angle. *Perameles* also resembles *Pucadelphys* in the high, thin, everted iliac wing, though it is relatively longer; but the ventral face of the ilium is wider, and there is practically no incisure in the acetabulum; the os marsupium is narrower than in *Pucadelphys,* being reduced to a rod; the distal ischiatic branch is also wider, hence the obturator foramen is smaller and the ventral puboischiatic carina is not salient. This carina is, on the contrary, very salient in *Monodelphis*, where the ilium is longer relative to the ischio-pubic part than in *Pucadelphys* and thicker than in *Metachirus*. Finally, the pelvis of *Didelphis* is more different, with a much longer and thicker ilium; the lateral ridge is very thick and the ventral face is ventroexternal; it has a relatively longer sacral surface for the two sacral vertebrae; the os marsupium is much wider distally. The pelvis of *Philander* is close to that of *Didelphis*, with a lower ilium and a short puboischium, but the very short os marsupium occupies only half of the anterior pubic border. The sutures between the three pelvic components are clear only in the subadult specimen of *Metachirus* used for comparison.

We conclude that *Pucadelphys* has a peramelid-like ilium, the dorsoventral anterior expansion of which we regard as a specialization, as well as the large size of the obturator foramen and the smallness of the os marsupium. But the relative shortness of the ilium and the massiveness of the ischio-pubic ensemble conform to what we infer to be the primitive state.

Femur. — In *Henkelotherium*, the femur is very similar to that of *Pucadelphys*; but the angle between the head and diaphysis is only 30° and there is no third trochanter. *Barunlestes* shows more differences: angle 60°, neck longer, greater trochanter higher, lesser trochanter less expanded proximodistally but more internally, internal condyle larger.

The femur of *Metachirus* is, as the humerus, more slender than that of *Pucadelphys*, with also a longer neck; the tuberosity internal to the trochanteric fossa is much more prominent, the greater trochanter reaches higher and there is hardly any third trochanter (the latter is said to be rare in marsupials: only three genera are mentioned by OSGOOD, 1921); finally, the slope of the distal border is quite steep, the medial condyle extending distally beyond that of the lateral condyle. The same remarks apply to *Didelphis*, where these features are more accentuated. The femur of *Philander* is robust and particularly wide distally; the neck and lesser trochanter are well developed, and the greater trochanter reaches the top of the head. The femur of *Monodelphis* resembles that of *Pucadelphys* in its proportions, its low greater trochanter and the quasi-absence of a neck, but the intertrochanteric fossa is less deep, the lesser trochanter is not so well developed though of the same shape and there is no third trochanter, no more than in *Perameles*; in this genus

Source : MNHN, Paris

the lesser trochanter is even more reduced, and shows again some specializations, particularly distally, that are probably related to fossorial adaptations. The fovea capitis occupies the same position in *Pucadelphys* and *Metachirus*, but it is better delimited and deeper in the latter; it is also faint in *Monodelphis* and poorly delimited, but situated higher on the head; it is eccentric in *Eozostrodon* too, less so in *Didelphis* and *Perameles*, but clearly circular.

Overall, the femur of *Pucadelphys* appears somewhat more generalized than those of the living didelphids.

Tibia-Fibula. — From the figurations, the tibia of *Henkelotherium* seems to have been more curved than in *Pucadelphys*; in any case this is true of *Metachirus*, where the bone narrows more in the distal half. But in the latter genus, the general morphology is very close to that of *Pucadelphys*, including details of the proximal surface and those of the internal face of the internal malleolus. One difference concerns the medial proximal facet, which is narrower, longer and deeper; these characters are even more accentuated in *Didelphis* and *Perameles*. The tibia of *Monodelphis* is also sigmoidal, narrower anteroposteriorly, but otherwise again very similar to that of *Pucadelphys*.

In *Barunlestes* the tibia and fibula are partly fused (an apomorphy found in some eutherians), and the tibia is more curved and narrower distally than in *Pucadelphys*.

In *Henkelotherium*, the fibula remains quite thick as in *Pucadelphys*. In *Metachirus* (and *Monodelphis*) the fibula is at the same time much more slender and more expanded proximally, and the tibial articular surface is less salient medially and distally. The specialisations toward fossorial adaptations observed on the femur of *Perameles* apply to the tibia-fibula. In all didelphids the two bones are completely and widely separated.

The fibula of *Pucadelphys* is clearly not as specialized as in living didelphids, being intermediate between those of the latter and that of *Henkelotherium*.

Astragalus. — The astragalus of *Pucadelphys* differs from that of *Didelphis*, where a short neck separates head and body: the condition in *Pucadelphys*, also present in *Caenolestes*, is considered to be primitive by Osgood (1921). The configuration of the two tibial facets suggests that the tibia of *Pucadelphys* was well locked with the astragalus so as to allow only slight lateral movements. Moreover, in *Didelphis* the CaA is more crescent-like, the interosseous relatively narrower and the condyle for the sustentaculum tali is more distinct. Dorsally the trochlear is even shallower but wider.

Only a very partial astragalus is preserved in *Henkelotherium*. That of *Barunlestes* is very different, with a distinct neck, and a medial ridge shorter than the lateral ridge. The astragalus of *Deccanolestes*, a placental from the late Cretaceous of India, is of interest in our comparisons because it has been shown by Godinot & Prasad (1994) to display arboreal specializations, in the trochlea (lateral crest higher than the medial crest, a condition opposite to that of *Pucadelphys*), in the angulation of the navicular facet relative to the sustentacular facet (again contrary to the situation of *Pucadelphys*).

Calcaneum. — The preserved part of the calcaneum of *Henkelotherium* is reduced to the tuber calcis. That of *Zalambdalestes* lacks a peroneal tubercle and the cuboidal facet is

Source : MNHN, Paris

perpendicular to the long axis of the bone, both states being more derived than those of *Pucadelphys*. In *Didelphis* (Fig. 51), the calcaneum has a relatively shorter heel, the sustentacular facet is clearly delimited (not in *Pucadelphys*) but there is no deep sulcus between it and the CaA; the long axis of the CaA (which is relatively less salient) is not so oblique relative to that of the heel. An important specialization of the calcaneum of didelphids is the plantar indentation which extends the cuboidal facet, itself completely terminal; the distoventral orientation of the cuboidal facet in *Pucadelphys* would thus seem to foreshadow the didelphid state.

The calcaneum of *Pucadelphys* is thus different from that of SZALAY's "metatherian morphotype" (1982a and b); in particular, the apparent absence of a fibular facet (CaFi, SZALAY, 1982) corresponds rather to his "didelphid morphotype tarsus", with a bicontact upper ankle joint (UAJ); however, this calcaneum resembles the plesiomorphic metatherian morphotype in having a large peroneal process and "remarkably broad transverse dimensions from peroneal process to the medial margin of the sustentaculum" (SZALAY, 1982a: 626). The presence of a large peroneal process is also mentioned in *Deccanolestes* (PRASAD & GODINOT, 1994) but is there interpreted as "related to powerful movements of inversion and eversion", hence to a very mobile foot; this character is indeed associated, in this genus, with other indicators of such a condition, for instance: difference in the size of the astragalar and calcanear caA, well rounded astragalar navicular facet.

Cuboid. — The cuboid of *Didelphis* is indented distally, and the articular surface for metatarsal V is better delimited. The greatest difference occurs ventrally, with the development of the proximal longitudinal process directed towards the secondary facet on the calcaneum. The intermeshing of cuboid and cuneiform III occurs in *Didelphis* and also in *Philander*.

Pes. — No tarsus of *Metachirus*, *Philander* or *Monodelphis* was available for comparison. The pes of *Perameles* is very specialized for digging, with a narrow tarsus and metatarsus.

In *Henkelotherium*, the metatarsals represent about 1/3 of the length of the tibia-fibula. In *Monodelphis*, the metatarsals equal less than 1/4 the length of tibia-fibula and the digits are interlocked proximally as in *Pucadelphys*. In *Philander*, the metatarsals are short (1/6th the length of tibia-fibula) and not linked to one another; II>III =IV>V. In *Didelphis*, the metatarsals, independent from one another, are only 1/5th the length of the tibia-fibula; III>II =IV>V.

Thus, the foot of *Pucadelphys* (where the metatarsals represent more than 1/3 the length of the tibia-fibula) was relatively long and rigid.

The proximal phalanges are almost as long as the metatarsals in *Henkelotherium* and *Philander*, slightly more than half as long in *Monodelphis* and *Didelphis* (and about half in *Pucadelphys*).

HABITS

About 22 species of mammals are known from Tiupampa, of which 50% are eutherian and 50% metatherian. As demonstrated by all skeletal and dental remains thus far collected, *Pucadelphys andinus* is the most abundant species of mammal in this fauna (MARSHALL & MUIZON, 1988).

Source : MNHN, Paris

Based on the adult specimens (6105 and 6106), *Pucadelphys andinus* measured about 135 mm from tip of snout to base of tail, and about 270 mm from tip of snout to tip of tail (assuming the presence of ±30 caudal vertebrae). In size it compares with some living species of *Marmosa* and with *Lestodelphis halli* (MARSHALL, 1977), and thus weighed about 50 grams.

LOCOMOTION. — Many living didelphids are terrestrial (*e.g. Lutreolina, Lestodelphis, Metachirus, Monodelphis*, some *Marmosa*) and those that have arboreal capabilities (*e.g.* some *Marmosa, Philander, Didelphis*) are often found on the ground. *Perameles* is specialized for digging and lives in burrows. From the above description, what can be deduced about the locomotion in *Pucadelphys*?

HILDEBRAND (1961) concluded from his study of body proportions in didelphids that the measurements of the various long bones did not yield any significant results: "the more arboreal animals differ from the semi-arboreal and terrestrial animals in behavior patterns but not in morphology". Also, JENKINS (1971) insisted justly on the importance of physiological factors in locomotion : "even if biomechanical conditions are similar, there may be profound differences .. in, for example, agility, in ratio or intensity of locomotor activity"; and in 1974, the same author noted: "the differences between arboreality and terrestriality of tree shrews is at times only behavioral". Finally, BARNETT & NAPIER (1953) wrote that "there is remarkably little morphologic difference between the form and mobility of the fibula in the ecologically distinct species (arboreal, unspecialized terrestrial and aquatic)". However, GRAND (1983) remarked that, whereas *Metachirus and Monodelphis* are both terrestrial, the hindlimb elongation in the former genus coincides with its agility and bounding locomotion; *Monodelphis*, with his subequal anterior and posterior limbs, remains effectively slower.

Before proposing locomotion capabilities of *Pucadelphys*, we shall summarize its skeletal characteristics:

1. Short spinous processes of the cervicals, are compatible with good flexibility of the neck.
2. Large dorsal metapophyses, long lumbar spinous processes as well as broad distal end of humerus are suggestive of digging abilities, while the same long and widely distant lumbar spines favor leaping capabilities (SLIJPER, 1946; GAMBARYAN, pers. comm., 1992).
3. The smallness of the space between ulna and radius suggests a very limited rotation of the forearm; the relation between the two bones seems to indicate a slight anteroexternal proximal superposition, a side-by-side position along the diaphyses and a slight anterointernal superposition distally.
4. The pelvis usually reflects locomotory specializations: leaping or digging forms have recognizable features on the bone, but these are extreme cases; for less specialized forms, interpretation is not so clear. Also, the shape of the pelvis not only depends on function but also on its relation to the viscera, as indicated by ELFTMAN (1929). In *Pucadelphys* we have noted a possible mobility of the sacro-iliac joint (as in *Perameles*); the broadness of the sacrum and the large ilio-sacral angle (both as in the digging form *Perameles)*; the wide, flat and laterally flaring surfaces for the erector spinae and gluteus medius (abductor and extensor of the thigh), again as in *Perameles*; similarly the pronounced downward curvature of the transverse processes of lumbar vertebrae corresponds to powerful erector spinae (ELFTMAN, 1929). The propulsive part part of the pelvis (behind the iliac

Source : MNHN, Paris

blade) is short, though not as short as in *Perameles*. The ischia are elongated to provide leverage for the hamstrings and increase the power of the adductors as extensors of the thigh as in leaping or digging forms; measurements for is/il ratio are: *Perameles*, 0.67; *Pucadelphys*, 0.53; *Didelphis*, 0.36; *Metachirus*, 0.47; *Monodelphis*, 0.37. All of these observations suggest digging capabilities for *Pucadelphys*. However, the posterior border of the ischium is slightly inclined forward and downward (while it is more vertical in *Perameles*): this can be interpreted as giving less strength to the extensors; also there is no strong buttress on the acetabulum, anteriorly or posteriorly (such a buttress is strong in digging forms), and finally the iliac muscle (which extends from the ventral surface of the ilium to the smaller trochanter and prevents the body from falling forward when digging) is esteemed to have been modest in *Pucadelphys*. But it should be kept in mind that there are many ways of digging and thus adaptive strategies can be different.

5. Relative limb proportions of *Pucadelphys*, with subequal fore- and hindlimbs, are intermediate between those of *Metachirus* and *Monodelphis*, and testify to a good agility (JULIEN-LAFERRIÈRE, 1991).

6. A tibia locked to the astragalus corresponds to a relatively rigid hindlimb (as opposed to an arboreal form); the relatively strong fibula (as in generalized marsupials: BARNETT & NAPIER, 1953) has only a limited distal contact with the tibia. Finally, the well developed internal and external malleoli usually indicate saltatorial capabilities (BARNETT & NAPIER, 1953)

7. The astragalus and calcaneum of *Pucadelphys* do not show arboreal specializations such as mentioned above (GODINOT & PRASAD, 1994), though the large peroneal process may indicate good mobility. The pes is relatively long, and it is deduced from the preservation of 6106 that the 1st digit (itself missing on the specimen) was at least slightly divergent; if not, one would assume that metatarsal I would have been preserved along with II and III (the big toe is only slightly divergent in *Monodelphis*, more so in *Metachirus*; note that divergence does not necessarily mean opposability, and simple opposability does not mean arboreality). Moreover, the united metapodials suggest a rigid pes: united digits and long metapodes are usually related to digitigrady, but the latter normally accompanies at least a reduction of digit I, a situation unknown in *Pucadelphys*. Finally, the configuration of the tibio-astragalus joint is not known; we thus ignore if it was such as to allow reversal of the foot, as observed by JENKINS & MCLEARN (1984) in some arboreal didelphids.

Based on the above, we prudently infer that *Pucadelphys* was essentially terrestrial, quite agile but neither cursorial nor saltatorial; it appears to have been capable of bounding and also of some digging, these two abilities being less developed than in *Metachirus* and *Perameles* respectively.

WAY OF LIFE. — *Pucadelphys* was probably nocturnal as are most living didelphids, sleeping in a burrow-nest during the day and foraging for food at night. Most living didelphids are solitary except during the breeding season (WALKER, 1964); MCMANUS (1970) stresses the poor social behavior of *Didelphis*. However, it is not uncommon that one individual would share a burrow with a congenere (or even a "foreigner", SHIRER & FITCH, 1970), especially in cold weather (didelphids with their naked ears, tail and paws are ill adapted to cold weather: FITCH & SHIRER,

Source : MNHN, Paris

1970) and also depending on the population density (CRAWLEY ,1973). Yet, there are no records that two males would huddle together (MCMANUS, 1970; SHIRER & FITCH, 1970). These observations suggest two interpretations for the specimen-pairs of *Pucadelphys andinus*: 1) they were male-female pairs that bonded for a restricted breeding season; or 2) that they were two females that shared the same burrow. For females of *Didelphis*, FITCH & SHIRER (1970) have observed that, "from time to time, two individuals were staying together in the same den simultaneously; on some occasions it seemed that the animals must have been side-by-side and in actual contact". A definitive choice between these two interpretations is not possible, as there are no features in either the skull or skeleton of didelphids which permit secure sexual identification [although in small mammals, females are often larger than males; WOOLLER *et al.*, 1981; but in *Trichosurus*, males are only 1% larger than females (CRAWLEY , 1973)]. Nevertheless, the occurrence of two specimen-pairs (i.e., a repeated association) of *Pucadelphys* at Tiupampa suggests the most natural and simplistic relationship (i.e. male-female pairs), rendering the first interpretation as most likely.

Ground nests of all of the mentioned didelphids have been found in hollow logs, under rocks or in burrows (WALKER, 1964). *Didelphis* curls in a den when it is cool, limbs close to the body, head under body; when very hot it lies on its back (MCMANUS, 1970). Thus, the "died-in-a-burrow" hypothesis (see above), and the three dimensional life-like position of the fossilized specimens are consistent with observed behavior and habits of some living didelphid taxa.

CONCLUSIONS

The vertebrate fauna from Tiupampa accumulated in channels of meandering rivers on a flat alluvial plain. The presence of several groups of crocodiles attests to a warm, probably subtropical climate. The fauna is from the middle member of the Santa Lucía Formation which, based on a detailed magnetostratigraphic study, would be between 59.5 and 59.0 Ma (SEMPERE *et al.*, in prep.).

The four specimens of *Pucadelphys andinus* described here represent the earliest and most complete articulated skeletons of metatherians yet known. The two sets of what are interpreted to be male-female pairs were found in a three dimensional, life-like, snout-rump position in burrow-nests that were apparently dug in a river bank. The animals probably died as the result of a flood which entrapped them in their burrows and filled the latter with water and sediment. Functional considerations of the skeletons suggest that *Pucadelphys* was essentially terrestrial, quite agile, and possessed limited bounding and digging capabilities. The vast majority of character states in the skeleton of *Pucadelphys* are regarded as mammalian, tribosphenic and metatherian plesiomorphies (i.e. atlas imperforate and with a persisting suture between ossified intercentrum and atlantal arch; absence of transverse canal on axis, with possible unfused rib; absence of enclosed transverse canal on CV7; strong fibula; presence of ossified os marsupium). The plesiomorphic states of the cervical vertebrae are not collectively found in any living didelphid examined.

Numerous other skeletal features of *Pucadelphys* also do not occur as a suite in any of the didelphids examined. These include: 1) a single fulcral vertebra (S2); 2) a long, non-prehensile

Source : MNHN, Paris

tail; 3) specialized lumbar series (gradual lengthening of vertebral body and transverse processes, and long anteriorly directed neural spines); 4) specialized pelvis (ilium dorsoventrally expanded anteriorly, large obturator foramen, small os marsupium); 5) possible movable sacro-iliac joint; and 6) digging specializations of the humerus [no third distal articular surface (OSGOOD, 1921), large areas for extensors of forearm and carpus]. Except for feature 2 and a small os marsupium (part of 4), the others are specializations reflecting the bounding and digging capabilities noted above.

The only postcranial element that reflects the phylogenetic position of *Pucadelphys* within Metatheria is the calcaneum. This bone has a bicontact upper ankle joint (UAJ) which is diagnostic of the family Didelphidae; moreover, the partially plantar orientation of the cuboidal facet can be interpreted as foreshadowing the state in living Didelphidae where the calcaneum has a distinct ventral indentation of the cuboidal facet. The calcaneum of *Pucadelphys* also approaches the "plesiomorphic metatherian morphotype" of SZALAY (1982a, b; 1984) in having a large peroneal process and remarkably broad transverse dimensions from peroneal process to the medial margin of the sustentaculum. This combination of tarsal states supports the interpretation based on the study of the skull, dentary and dentition (MARSHALL & MUIZON, this volume) that *Pucadelphys* represents the most plesiomorphic taxon within the family Didelphidae.

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Source : MNHN, Paris

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Source : MNHN, Paris

APPENDIX: measurements

In the following tables, all measurements (in mm) are of specimens of *Pucadelphys*. The abbreviation *ca.* is used in the sense of "estimated". But it should be made clear that all measurements are to be taken with caution, the figures obtained depending on the orientation and focus choosen by the operator.

Dans les tableaux suivants, toutes les mesures (en mm) sont celles de Pucadelphys andinus. *L'abréviation* ca *indique qu'il s'agit d'une estimation. Mais toutes ces mesures doivent être considérées avec prudence, les valeurs obtenues dépendant en partie de l'orientation et de la mise au point choisies par l'opérateur.*

TABLE 1. — Measurements of atlas and axis.
TABLEAU 1. — *Mesures de l'atlas et de l'axis.*

specimen		6105	6110
Atlas (CV1):			
	Width of axoidian facet	1.5	1.3
	Mxm length of arch	2.0	2.4
	Ventral length	0.9	1.2
Axis (CV2):			
	Length of neural arch	4.1	4.2
	Mxm length	5.4	4.7
	Height of dens	0.7	0.5
	Width of dens	1.2	1.1
	Height of neural arch	ca. 3.9	ca. 3.9
	Mxm width at atlantal articulation	5.0	4.4
	Width of tv.proc. (dorsal root) as preserved	8.0	
	Posterior width of centrum	2.8	2.4

TABLE 2. — Measurements of cervical vertebrae 3 to 7.
TABLEAU 2. — Mesures des vertèbres cervicales 3 à 7.

specimen			6105
CV 3	Centrum:	Length	2.4
		Anterior width	2.4
		Posterior width	2.6
CV 4	Centrum:	Length	2.0
		Anterior width	2.8
		Posterior width	2.6
CV 5	Centrum:	Length	1.8
CV 6	Centrum:	Length	1.7
CV 7	Centrum:	Length	1.65

Source : MNHN, Paris

TABLE 3. — Measurements of thoracic vertebrae.
TABLEAU 3. — Mesures des vertèbres thoraciques.

specimen			6105	6106	6110	6111
T1	Centrum:	Length	2.3	2.4		
		Anterior width	2.9	1.9		
		Posterior width	2.3	2.0		
	Width of transverse processes		8.4	6.8		
T2	Centrum:	Length	2.4	2.4		
		Anterior width	2.3			
		Posterior width	2.8			
	Width of transverse processes		ca. 5.0			
T3	Centrum:	Length	2.5	2.7		
	Width of transverse processes			ca. 5.0		
T4	Centrum:	Length	2.75	2.7		
T5	Centrum:	Length	2.6	2.9		
T6	Centrum:	Length	2.55	2.8	2.2	
		Anterior width			ca. 1.6	
		Posterior width			ca. 1.8	
T7	Centrum:	Length	2.0	3.0	ca. 2.2	
		Anterior width			ca.1.6	
		Posterior width			ca. 1.7	
T8	Centrum:	Length	2.6	3.0	2.2	
		Anterior width			ca. 2.0	
		Posterior width			ca. 2.0	
T9	Centrum:	Length	ca. 2.8	3.0	2.3	ca. 1.9
		Anterior width			ca. 2.1	
		Posterior width			ca. 2.2	
T10	Centrum:	Length		3.1	2.3	ca. 1.9
T11	Centrum:	Length		3.1	2.4	ca. 2.0
T12	Centrum:	Length		3.2	2.45	2.4
T13	Centrum:	Length		3.6	2.65	2.5

Source : MNHN, Paris

TABLE 4. — Measurements of lumbar vertebrae.
TABLEAU 4. — Mesures des vertèbres lombaires.

specimen			6106	6110	6111
L1	Centrum:	Length	3.7	3.0	2.5
		Anterior width	3.0		2.0
		Posterior width	3.6		ca. 2.4
	Width of transverse processes		4.0		
L2	Centrum:	Length	4.5	3.0	ca. 2.9
		Anterior width	2.9		
		Posterior width	2.8		
	Width of transverse processes		5.0		
L3	Centrum:	Length	4.9	3.8	ca. 3.3
		Anterior width	2.8	4.0	
		Posterior width	3.0		
	Width of transverse processes		5.6		
L4	Centrum:	Length	5.3	3.8	3.3
		Anterior width	2.8		
		Posterior width	3.1		
	Width of transverse processes		6.5		
	Length of spinous process		4.00		
L5	Centrum:	Length	5.0	3.5	3.7
		Anterior width	3.0		
		Posterior width	4.5	3.1	
	Width of transverse processes		6.9		
	Length of spinous process		4.20		
L6	Centrum:	Length	4.3	3.0	ca. 2.9
		Anterior width			
		Posterior width	3.9	2.5	
	Width of transverse processes		8.1		
	Length of spinous process		4.90		

TABLE 5. — Measurements of sacral vertebrae.
TABLEAU 5. — Mesures des vertèbres sacrées.

specimen			6106	6110	6111
S 1 + S 2	Length		7.4	6.5	5.5
S 1	Centrum:	Length	3.4	3.1	ca. 2.5
		Anterior width		2.5	
		Posterior width	3.0	2.3	ca 1.9
	Width of transverse processes between pelves		10.0	8.4	6.6
S 2	Centrum:	Length	4.0	3.4	ca. 2.5
		Anterior width	3.0	ca. 2.3	
		Posterior width	3.0		
	Sacral foramen:		(l)	(r)	
		Length	1.0	1.05	
		Width	1.0	1.0	

Source : MNHN, Paris

TABLE 6a. — Measurements of caudal vertebrae (C1 - C9).
TABLEAU 6a. — Mesures des vertèbres caudales (C1 - C9).

specimen			6106	6110	6111
C 1	Centrum: Length		3.7		ca. 2.3
	Anterior width		2.5		
	Posterior width		2.6		
C 2	Centrum: Length		3.7		ca. 2.3
	Anterior width		2.5	2.2	
	Posterior width		2.7	ca. 2.25	
	Width of transverse processes		ca. 10.0		
C 3	Centrum: Length		3.5		2.8
	Anterior width				
	Posterior width			2.1	
	Width of transverse processes		ca. 9.8	ca. 5.5	
C 4	Centrum: Length		3.5	ca. 2.6	2.5
	Anterior width			1.9	
	Posterior width		3.0	1.7	2.4
	Width of transverse processes		9.0	ca. 6.6	5.6
C 5	Centrum: Length		4.0	ca. 3.5	3.3
	Anterior width		2.4	1.9	1.9
	Posterior width		2.1		2.2
	Width of transverse processes			ca. 5.4	6.0
C 6	Centrum: Length		5.5		4.3
	Anterior width		2.15		2.1
	Posterior width		2.9		2.5
	Width of transverse processes		ca. 7.0		4.4
C 7	Centrum: Length		7.0		5.0
	Anterior width		2.7		2.2
	Posterior width		3.0		2.2
	Width of transverse processes:	anterior	4.1		4.8
		posterior	ca. 6.0		
C 8	Centrum: Length		7.7		6.9
	Anterior width		2.6		2.5
	Posterior width		2.1		2.3
	Width of transverse processes:	anterior	5.8		
		posterior	4.6		
C 9	Centrum: Length		8.0		
	Anterior width		2.4		2.2
	Posterior width		2.3		
	Width of transverse processes:	anterior	4.6		
		posterior	4.0		

Source : MNHN, Paris

TABLE 6b. — Measurements of caudal vertebrae (C16?, C17?, C20?, C21?).
TABLEAU 6b. — Mesures des vertèbres caudales (C16?, C17?, C20?, C21?).

specimen				6110
C 16?	Centrum:	Length		ca. 6.5
		Anterior width		1.9
		Width of transverse processes:	anterior	2.9
C 17?	Centrum:	Length		7.0
		Anterior width		1.4
		Posterior width		1.4
C 20?	Centrum:	Length		6.1
		Anterior width		1.4
		Posterior width		1.6
C 21?	Centrum:	Length		6.4
		Anterior width		1.3
		Posterior width		1.2

TABLE 7. — Measurements of scapula.
TABLEAU 7. — Mesures de l'omoplate.

specimen	6105	6106	
	(l)	(l)	(r)
Length	ca. 15.0		ca.18.0
Maximum proximal width		3.8	4.0
Width of glenoid fossa		ca. 2.0	ca. 2.0

TABLE 8. — Measurements of clavicle.
TABLEAU 8. — Mesures de la clavicule.

specimen	6105	6110	
	(l)	(l)	(r)
Length	10.5		
Width of sternal end	2.0	ca. 1.8	
Width of scapular end	1.1		1.2
Median width	0.9	0.8	0.7

Source : MNHN, Paris

TABLE 9. — Measurements of interclavicle.
TABLEAU 9. — Mesures de l'interclavicule.

specimen	6105
Total length	8.9
Length anterior to costal tuberculae	3.1
Length posterior to costal tuberculae	5.0
Width of end cephalic	1.2
caudal	1.4
Width between costal tuberculae	3.7

TABLE 10. — Measurements of humerus.
TABLEAU 10. — Mesures de l'humérus.

specimen	6105 (l)	6106 (l)	6110 (l)	6110 (r)
Length	17.5	20.7	ca. 16.3	17.0
Transverse width proximal end				3.8
Ant.-post. width proximal end		3.7	3.75	3.4
Transverse width distal end	6.3	6.0		4.5

TABLE 11. — Measurements of ulna.
TABLEAU 11. — Mesures du cubitus.

specimen	6105 (l)	6106 (l)	6110 (l)	new specimen (r)
Length of olecranon + sigmoid cavity			ca. 4.6	5.0
Length of sigmoid cavity		1.9	1.8	2.5
Depth of olecranon at mid-length		1.6	2.1	2.0
Depth of sigmoid cavity at mid-length	1.9	1.9	1.7	1.7

TABLE 12. — Measurements of radius.
TABLEAU 12. — Mesures du radius.

specimen	6105 (l)	6110 (l)
Length		ca. 14.0
Width of proximal articular surface	1.65	
Minimum width of diaphysis	1.1	

Source : MNHN, Paris

TABLE 13. — Measurements of pelvis.
TABLEAU 13. — Mesures du bassin.

specimen		6106 (l)	6110 (l)	6111 (l)	6111 (r)
Length (ant. edge of ilium to post. edge of ischium)		24.0			18.0
Width between iliac wings (ant. width)		17.0			ca. 10.0
Width between lateral edges of ischium (post. width)		13.0			ca. 10.0
Length of pubic symphysis		10.0			ca. 8.0
Length of ilium		ca. 10.0		10.0	ca. 9.0
Length of ischium			ca.8.0	8.8	9.0
Width of post. end of ischium			ca.4.5	4.5	
Obturator foramen	Length	6.8			
	Width	4.2			

TABLE 14. — Measurements of os marsupium.
TABLEAU 14. — Mesures de l'os marsupial.

specimen	6106 (l)	6106 (r)
Length	9.3	
Width of contact with pelvis	3.1	3.2

TABLE 15. — Measurements of femur.
TABLEAU 15. — Mesures du fémur.

specimen	6106 (l)	6106 (r)	6110 (l)	6110 (r)	6111 (l)	6111 (r)
Length	25.0	24.5	ca. 20.0	21.0	19.3	19.0
Proximal transverse width	5.7	5.8	5.6			4.5
Distal transverse width	ca. 4.4	4.3	4.3	4.0		
Distal ant.-post. width	3.6	3.5	ca.3.6	ca.3.8	3.1	

Source : MNHN, Paris

TABLE 16. — Measurements of tibia.
TABLEAU 16. — Mesures du tibia.

specimen	6105	6106		6110	6111
	(l)	(l)	(r)	(l)	(r)
Length	23.5		26.5		ca. 19.0
Proximal transverse width	3.7		3.8	4.0	
Proximal ant.-post. width	3.3	3.4	3.5	ca. 3.1	
Transverse distal width	3.3	ca. 3.1	ca. 3.1		2.2

TABLE 17. — Measurements of fibula.
TABLEAU 17. — Mesures du péroné.

specimen	6105	6106		6110	6111
	(l)	(l)	(r)	(l)	(l)
Length	ca. 22.5		ca. 24.5		
Proximal transverse width	ca. 3.0	ca. 3.0		2.6	
Proximal ant.-post. width	1.9				
Transverse distal width		2.3	2.4		2.0
Ant.-post. distal width	2.0				1.7

TABLE 18. — Measurements of calcaneum.
TABLEAU 18. — Mesures du calcanéum.

specimen	6106		6110	6111
	(l)	(r)	(r)	(l)
Length	5.3	5.6	4.2	ca. 4.0
Width of tuber	1.5	1.6		
Distal width	4.0			

Source : MNHN, Paris

TABLE 19. — Measurements of tarsals.
TABLEAU 19. — Mesures des tarsiens.

specimen		6105 (l)	6106 (r)	6110 (l)
Cuboid:				
	Length (dorsal length)	1.6	2.3	1.6
	Distal width	1.65	1.5	1.5
Cuneiform IV:				
	Length (dorsal length)			1.0
	Distal width			0.6

TABLE 20. — Measurements of metapodials.
TABLEAU 20. — Mesures des métapodes.

specimen	6105 (l)	6106 (r)	6110 (l)
Metapodial II:			
Length	7.0		ca. 6.5
Proximal width	0.9		0.8
Distal width	1.5		ca. 1.25
Metapodial III:			
Length	7.5	ca. 8.0	ca. 7.0
Proximal width	1.1	1.1	0.8
Distal width	1.5	1.4	
Metapodial IV:			
Length	ca. 7.5	8.0	ca 7.0
Proximal width		1.1	
Distal width		1.6	
Metapodial V:			
Length	6.0	6.3	
Proximal width	2.15	2.5	
Distal width	1.2		
Proximal phalanx:	3.4		

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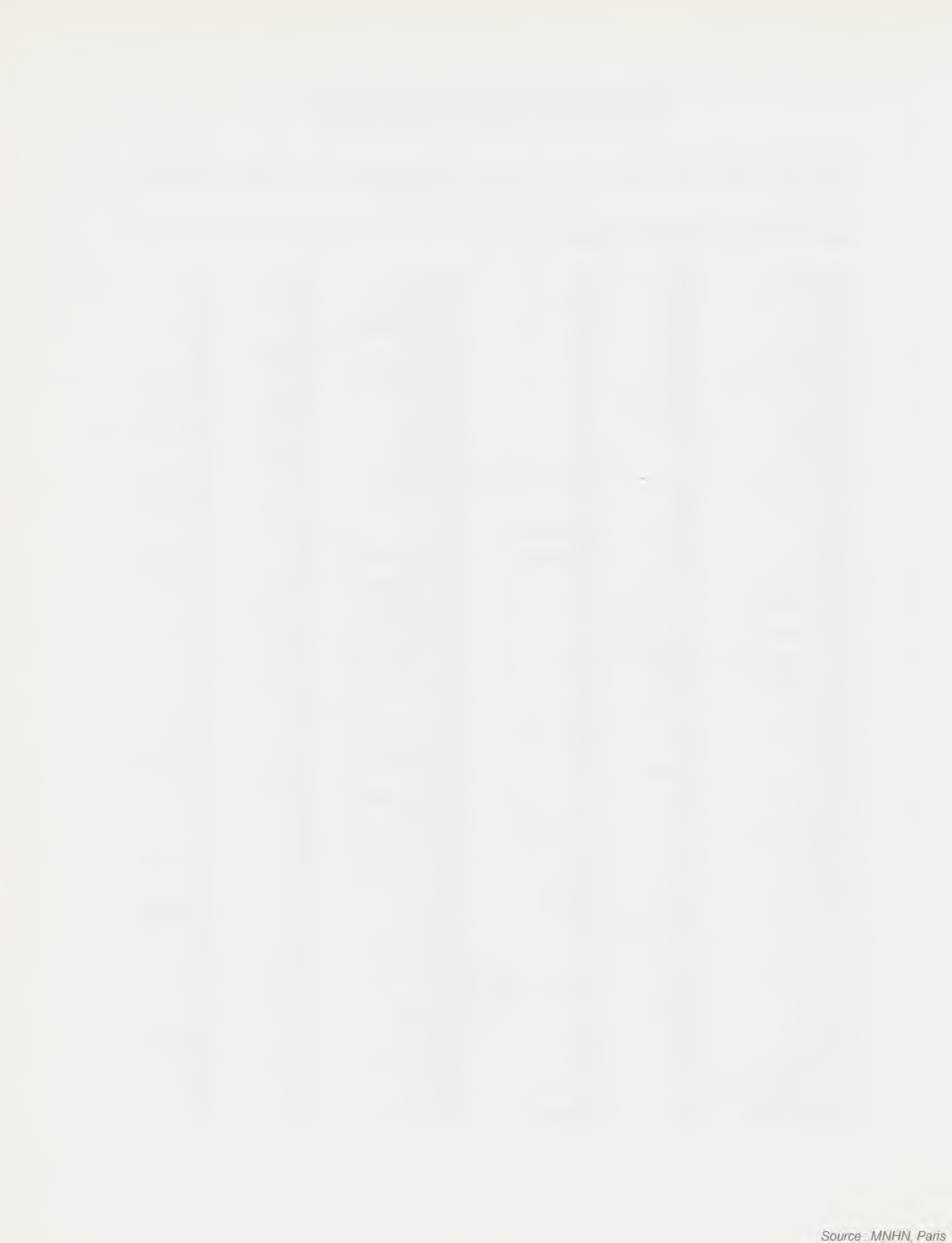

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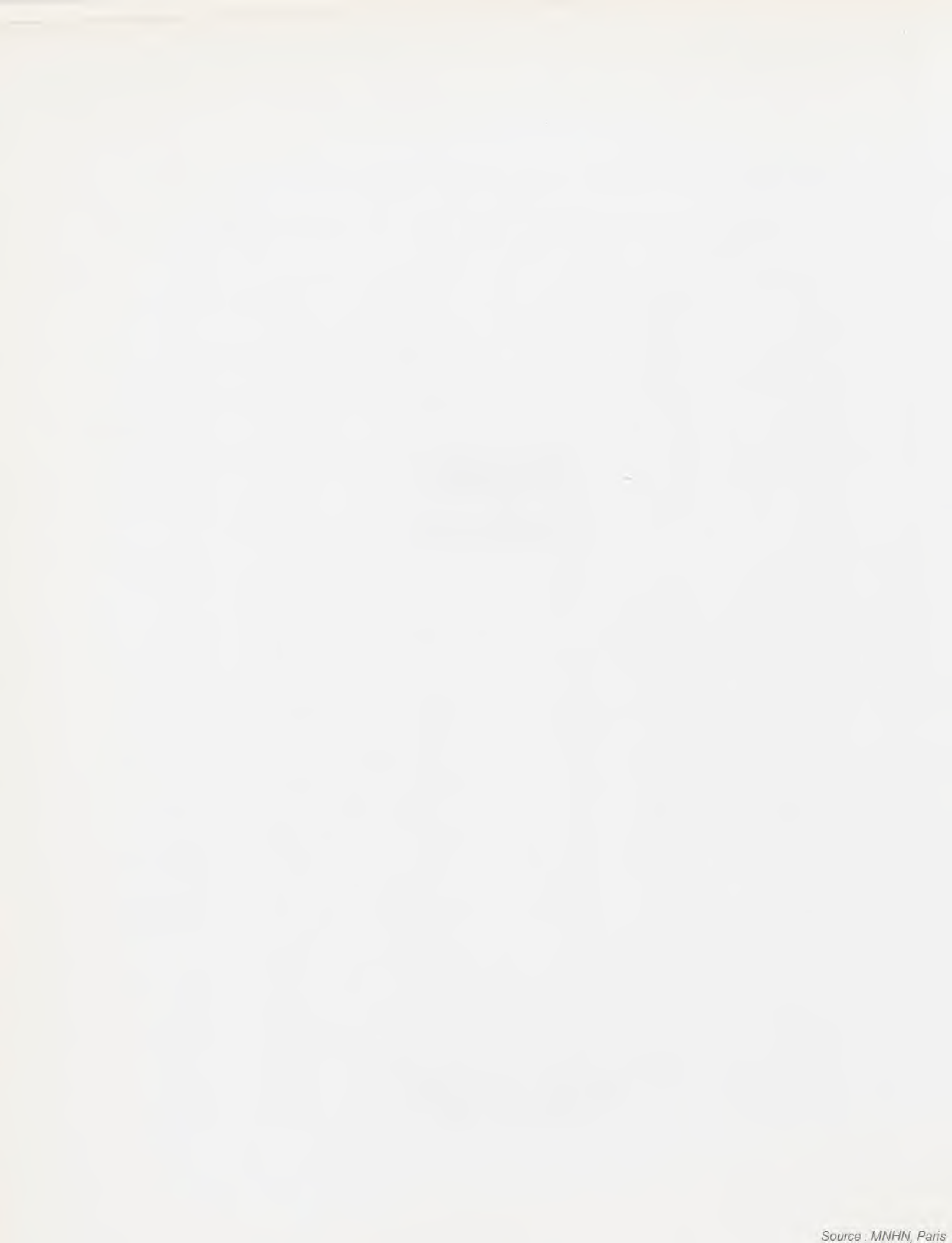

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